

# ORTHAMBONITES AND RELATED ORDOVICIAN BRACHIOPOD GENERA

by VALDAR JAANUSSON *and* MICHAEL G. BASSETT

**ABSTRACT.** In a revised diagnosis, *Orthambonites* is restricted to a small group of late lower Ordovician (latest Arenig-Llanvirn equivalent) brachiopods from Baltoscandia. *Orthambonites rotunda* is proposed as the formal type species of the genus to replace *Orthambonites transversa* which is considered a *nomen dubium*. Revision of *Orthis calligramma* suggests in turn that it is a senior subjective synonym of *O. rotunda*, and thus becomes the effective type species of *Orthambonites*. Many species included previously within the genus are assigned to *Paralenorthis*, and to three new genera – *Sulevorthis*, *Sivorthis*, and *Shoshonorthis*. *Krattorthis* is defined as a new related genus. Neotypes are proposed for *O. rotunda* and *Sulevorthis lyckholmensis*. A lectotype is designated for *Orthis callactis*, the type species of *Orthis*, which is discussed briefly in order to clarify past confusion with *Orthambonites*.

ONE of the most commonly quoted Lower Palaeozoic brachiopod genera in recent palaeontological literature is *Orthambonites* Pander, 1830. For many years this genus was regarded generally as a junior subjective synonym of *Orthis* Dalman, 1828, until Cooper (1942, p. 229) revived the use of the name *Orthambonites* to embrace a wide range of coarsely ribbed, biconvex, orthacean species. However, the relationships of these many species to type material of the genus have remained poorly understood, not least because Pander's original collections from the Ordovician of Ingria (St Petersburg district, Russia – also known by its Swedish name as Ingermanland) have been lost for well over a century (see below, pp. 23, 33). Cooper (1956, p. 294) recognized the likelihood that in its revived concept the genus is composite, and in working mainly on various Ordovician faunas from Baltoscandia we also concluded separately that a number of stocks are involved for which there remains a great amount of taxonomic imprecision and nomenclatorial confusion at both the generic and specific levels. This paper incorporates our combined data to revise some definitions and relationships within the '*Orthambonites* group' in the Baltoscandian area, and in turn this re-evaluation has enabled us to review the wider geographical and stratigraphical limits of the taxa involved.

Of particular importance for this study have been the extensive collections of orthacean brachiopods from Ingria housed in the Naturhistoriska Riksmuseet, Stockholm, the CNIGR museum and at VSEGEI in St Petersburg, and in the Institute of Geology in Tallinn, Estonia. These collections were made at various times during the nineteenth and twentieth centuries and are mostly from sections in the type area from where Pander's species were described, between the rivers Izhora and Ligovka to the south of St Petersburg (see Pander 1830, pl. 1, figs 1–3 and his un-numbered map). Some later authors such as Murchison *et al.* (1845, pp. 20, 28) and Schmidt (1897, p. 5) gave brief additional information on these sections in sketch maps and vertical profiles and commented on the faunas, but precise locality details for Pander's taxa remain unknown. We have also studied additional collections from Ingria from around Izvos on the Volkhov river some 120 km to the east-north-east of Pander's sections, from where contemporaneous brachiopods relevant to this paper have been described more recently (e.g. Alikhova 1953; Rubel 1961).

On the basis of all these collections it has been possible to try to assess some of the probable variation encompassed within Pander's (1830) very narrow species concept, which it is otherwise difficult to interpret only from his very short descriptions and his drawings of small shells at natural size; it should be noted, however, that in most cases Pander's illustrations appear to be fairly

accurate representations of the specimens (as opposed to species) that he described, particularly with regard to number of ribs and general outline and convexity.

From the literature, we have noted some seventy species described within Cooper's (1942) broad definition of *Orthambonites*. The majority of these differ clearly from the distinctive but restricted group of fairly large Baltoscandian late lower Ordovician species to which we restrict the genus in this paper, typified by *O. calligramma* Dalman, 1828. Many of the described biconvex species can be assigned fairly readily to other genera that we discuss here, but there still remain some twenty forms that are either poorly described, inadequately illustrated, based on poorly preserved specimens, or have somewhat deviating external features and no information on internal morphology; the generic reference of these cannot be determined at present (see also p. 58).

*Note on terminology.* In reference to stratigraphy and faunal distributions throughout this paper we use the terms 'lower', 'middle' and 'upper' for the Ordovician System only in an informal sense, but for consistency we relate this usage to the tripartite subdivision as applied commonly in Baltoscandia (for summary see Jaanusson 1982, p. 8, fig. 4). Because of imprecision in inter-regional and intercontinental correlations within the Ordovician, and in the absence of a globally applicable chronostratigraphical subdivision of the System, we record the distributions of genera and species in current local terminology appropriate to any particular region (mostly by reference to a Formation and/or to a 'regional Stage' or 'regional Series'). In some cases, where sufficiently precise data are available to allow correlation with the graptolite zonation, we refer to the graptolite succession determined in Skåne [Scania], southernmost Sweden (e.g. Jaanusson 1982, fig. 4). Apart from in the lower Ordovician, this zonation is close to that of the British standard succession, but in Skåne the definition of zonal boundaries is generally more precise, and correlation based on this region also has the advantage of giving close ties to the Ordovician North Atlantic conodont zonation (Bergström 1971*b*, 1986). For the many species referred to *Orthambonites* from the southern Appalachians of the USA (Cooper 1956), we base our age data on Ross *et al.* (1982), Jaanusson and Bergström (1980, fig. 7), and Bergström (1971*a*, fig. 10).

Morphological terminology follows that of Williams *et al.* (1965), with the addition of terms used by Jaanusson (1971) for hinge-teeth. Many papers refer to ribbing strength and patterns in brachiopods in a loose sense; differences in ribbing styles are important diagnostic characters in some of the taxa discussed here, and we emphasize our consistent differentiation between costae (first order ribs originating in the umbonal area), costellae (second order ribs arising by implantation or bifurcation beyond the umbonal area), and capillae (very fine radial ribs generally as micro-ornament on costae, costellae and in the interspaces between them). In referring to the relative dimensions of interareas, some authors use the term 'height' and others 'length' for the parameter taken sagittally from the centre of the hinge to the tip of the beak; we refer to this as the length of the interarea as it is measured sagittally along the length of the shell, and its true height is partly a function of its attitude relative to the commissural plane. All dimensions are given in millimetres (mm).

## SYSTEMATIC PALAEOLOGY

Superfamily ORTHACEA Woodward, 1854

Family ORTHIDAE Woodward, 1854

Subfamily ORTHINAE Woodward, 1854

Genus ORTHAMBONITES Pander, 1830

*Discussion of type species.* Under ICZN rules the formally designated type species of *Orthambonites* is *O. transversa* Pander, 1830 (subsequent designation by Schuchert and LeVene 1929, p. 90; some authorities refer to an earlier designation by Dall 1877, p. 51, but this is not valid as Dall only referred to the name as Pander's first listed species without specifying it as the type). In following previous usage, this species was in fact probably selected because it was the first in the list of seventeen nominal species of *Orthambonites* described by Pander and thus had page priority (Pander 1830, p. 81, pl. 22, fig. 1; an eighteenth species was named and figured by Pander on his pl. 16A, fig. 4 as *O. dubia*, but this was not described in the text; see also pp. 56–57 herein). However, as noted by Öpik (1934, p. 130), within each genus in his monograph Pander listed the assigned species consistently in a morphological series, beginning with what he considered as least 'typical'

for the genus or even transitional to another genus. The most 'typical' representatives were normally listed in the middle of the sequence of species, and for this reason the first named taxon is usually a poor choice for the type of a brachiopod genus erected by Pander. Such an argument applies in the case of *Orthambonites*, to the extent that no author since Pander has described or illustrated material as '*O. transversa*' and it remains impossible to make such an identification with any certainty based only on the original illustrations and description. It is not unlikely that the original described and figured specimen (Pander 1830, p. 81, pl. 22, fig. 1) is an extreme variant in the morphological range of a species; in particular, the dorsal valve of this specimen is more strongly convex than is typical for Ingrian forms with the same size, outline and number of ribs. The material described in Pander's monograph is lost and is presumed to have been destroyed (L. E. Popov pers. comm.), so that without the possibility of examining characters of the original specimen that are unclear or are not shown on the figures, '*Orthambonites transversa* Pander, 1830' must be considered a *nomen dubium*.

Prior to Cooper's (1942, 1944, 1956) revival of the genus, this uncertainty as to the status of the type species was essentially academic since, as noted above, from almost immediately after its description by Pander it was generally regarded as synonymous with *Orthis*, following authorities such as Buch (1840*a*, 1840*b*), Eichwald (1840), Verneuil (*in* Murchison *et al.* 1845, p. 207), Bronn (1848, p. 852), Dall (1877, pp. 36–51), Hall and Clarke (1892, pp. 186, 236), Schuchert and LeVene (1929, p. 90), and Schuchert and Cooper (1932, pp. 75–76). Nomenclatorial confusion accompanying this synonymy was introduced by Buch (1840*a*, p. 206; 1840*b*, p. 18) when he used Pander's generic name *Orthambonites* as a specific name within the genus *Orthis*, and Pander's nominal species were all submerged within '*Orthis orthambonites*'; Eichwald (1840, p. 150) adopted Buch's usage, and then Verneuil (1845, p. 207) took the nomenclature one stage further in naming *Orthambonites* as a 'variety' of the Swedish species '*Orthis calligramma* Dalman, 1828'. Later authors tended to use only *calligramma* as a species name, with *Orthambonites* generally being synonymized within *Orthis*.

In this context it is important to note that in describing his many species for his 1830 monograph, Pander had not seen Dalman's 1828 publication and the original description of *Orthis* and *O. calligramma* (he makes no mention of Dalman's paper in the introduction, although he does refer to earlier work by the same author). Some evidence from later collections available to Pander suggests that he too subsequently accepted many of his *Orthambonites* species as synonyms of *O. calligramma* (see p. 33).

Schuchert and Cooper (1932, pl. 2, caption to figs 8, 12, 15) hinted that *Orthis* and *Orthambonites* might be separable following further study, but did not take that step at that time. With only a few exceptions, such as the brachiopod volume of the Soviet *Osnovy Paleontologii* (Alikhova *in* Sarycheva 1960, p. 187), Cooper's subsequent separation of the two genera has been generally adopted, but in the absence of data on the morphology of the type species, *Orthambonites* has usually been interpreted in relation to *O. calligramma*. Rubel (1961, p. 173) even listed *calligramma* as the type species of *Orthambonites*, but since this was not one of the taxa included originally in the genus by Pander it cannot qualify objectively as the type. Problems of generic definition have also been compounded by the fact that *O. calligramma* itself has been interpreted within rather broad morphological limits and has not been described or illustrated adequately on the basis of type material subsequent to its original description from high lower Ordovician beds in southern Sweden (Dalman 1828); the species name has been applied to numerous Ordovician and Silurian forms or 'varieties' from many parts of the world (e.g. Giovannoni and Zanfra 1979, table 1 and fig. 7).

From our examination of Ingrian collections, we consider that some material described from the region by previous writers as *Orthambonites calligramma* (Alikhova 1953; Rubel 1961) in fact closely matches Pander's description (1830, p. 82) of *Orthambonites rotunda*. In this respect there is one important anomaly between Pander's text and illustrations, despite their otherwise apparent accuracy as noted above; his description of *O. rotunda* states that it has 'at least thirty ribs', whereas on the illustration (Pander 1830, pl. 22, fig. 5) there are only 26 distinct ribs; for the following species, *O. aequalis*, he stated (p. 82) that there are 'twenty-six flat ribs', whereas in this case the

illustration (pl. 22, fig. 6) has 30 (possibly 31) ribs. This is the only such anomaly of which we are aware in Pander's brachiopod descriptions. It appears to us therefore that in this example the descriptions and figures have become transposed; we here regard the description as having page priority and thus being definitive. Despite the somewhat typological application of these figures of rib numbers, it is important in this historical context to understand Pander's own concept of his species in order now to apply his nomenclature. Thus we interpret Pander's original specimen of *rotunda* as having about 30 primary ribs.

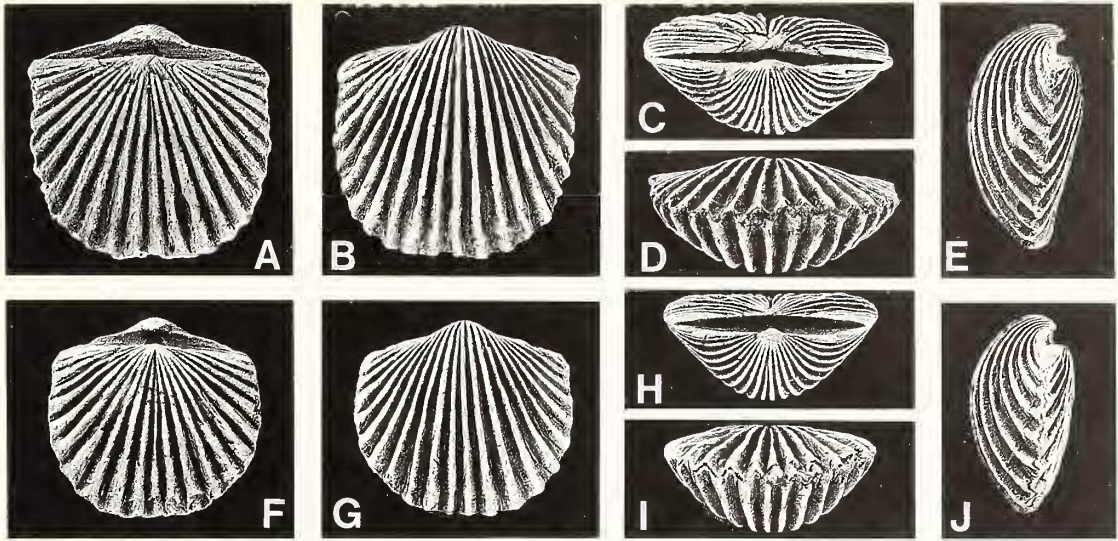
Given that specimens occurring commonly in Ingria can now be matched with *O. rotunda*, and that this is one of Pander's original species included in *Orthambonites*, with a morphology that satisfies the accustomed usage of the genus, it appears to be the best choice as a substitute type species; it is also from the middle part of the list of Pander's species of *Orthambonites* and can therefore be assumed to represent what he considered as a 'typical' form. With regard to the accustomed usage, it should be noted that, for example, this species from Ingria was used to typify the genus *Orthambonites* in the *Treatise on Invertebrate Paleontology* (Williams in Williams *et al.* 1965, fig. 196: 4a-e; taken from Alikhova 1953 and named, following her, as *O. calligramma*).

In order to stabilize the concept of the genus we are submitting an application to the ICZN to set aside previous designations and to rule that the type species of *Orthambonites* be designated as *Orthambonites rotunda* Pander, 1830.

The corollary to this formal requirement of designating one of the originally named species as the type species (ICZN 1985, Articles 67g, 69ai) is discussed further below (pp. 25, 33) in consideration of the relationships of *O. rotunda* and *O. calligramma*. It is sufficient at this point to note that we consider *rotunda* to be a junior subjective synonym of *calligramma*, so that the latter will effectively act as the type species for practical, comparative purposes.

It is also relevant here to discuss two further species named by Pander (1830) which have added confusion to the interpretation of *Orthambonites*. The Stockholm collections from Ingria include a number of specimens whose general size range, convexity, relative length of interareas, and number and style of ribs agree with illustrations of *Orthambonites tetragona* Pander (1830, p. 81, pl. 22, fig. 3a-d), and whose range of variation also encompasses shells similar to Pander's illustrations of *Orthambonites rotundata* (Pander 1830, p. 81, pl. 22, fig. 4a-d). It has been suggested that *O. transversa* is conspecific with *O. rotundata* (Öpik 1939, p. 122) or with both *O. rotundata* and *O. tetragona* (Alikhova 1953, p. 31). However, material of the two latter forms identified by us (all named here as *tetragona*, the senior name by page priority) clearly does not belong to *Orthambonites* of accustomed usage and as diagnosed in this paper; *tetragona* is a fairly small species (known maximum length 15 mm) with weak dorsal curvature, 20-23 strong costae, and distinct concentric fila but no trace of radial capillae. Rubel (1961, pl. 19, figs 1-5) described and figured conspecific shells as *Glossorthis* sp. a, and the exterior features certainly have a general similarity to this genus (Rubel recorded 26 costae but in the specimen in question - his pl. 19, fig. 2 - the ornament at the dorsal left cardinal angle is abnormal, possibly due to slight injury). Alikhova (1969, p. 25) questioned the reference of Rubel's specimen to *Glossorthis* and suggested that it may represent a juvenile shell of *Orthis* (i.e. including *Orthambonites* in her sense), but on the basis of the absence of capillate ornament this is certainly not correct. One reason for Alikhova's doubt was that she (1969, p. 25) considered *Glossorthis* to be restricted to the lower half of the middle Ordovician (Viru Series), whereas Rubel's specimen is from the immediately underlying beds (Kundan Stage, Aluojan Substage). However, in the Stockholm collections '*O.*' *tetragonus* occurs in association with other species indicating a basal Viru (Aserian) age, and it is likely therefore that the species ranges from the Aluojan Substage to the Aserian Stage. We have no information on the internal features of *tetragonus* so that its generic reference must remain uncertain, but on the basis of its external morphology (Text-fig. 1) we believe tentatively that Rubel's (1961) assignment of this form to *Glossorthis* is possible though not yet proved.

If *O. transversa* were to be retained as the type species of *Orthambonites*, and if Öpik's (1939) and Alikhova's (1953) views were supported as to its synonymy with '*O.*' *rotundata* and '*O.*' *tetragona*, then this would mean that *Orthambonites* would become restricted to quite a different group of



TEXT-FIG. 1. *Glossorthis?* *tetragona* (Pander, 1830); dorsal, ventral, posterior, anterior and lateral views of two conjoined shells demonstrating differences from *Orthambonites* in external morphology (see text for discussion). A–E, RM Br73943; F–J, RM Br73944. Both from Pulkova, Ingria, exact horizon unknown,  $\times 2$ .

orthaceans than in common usage, and it may even prove to be a senior subjective synonym of *Glossorthis* Öpik, 1930. This serves further to emphasize the status of *O. transversa* as a *nomen dubium* and lends support to an unambiguous definition of *Orthambonites* based on *O. rotunda* [= *calligramma*].

#### Generic diagnosis of *Orthambonites*

Subequally biconvex to ventribiconvex, curvature moderate to strong, anterior commissure rectimarginate, shells relatively large, ventral interarea short, concave, weakly apsacline to orthocline. Ornament costate or rarely with very few costellae (known range 19–37 ribs in adult specimens), fine capillae and concentric fila well developed. Ventral vascula media long, straight, closely adjacent and parallel for much of their extent proximally. Dental plates suberect to receding, ventral muscle field extends only slightly anterior to delthyrial cavity, anterior margin gently rounded to weakly lobed. Cardinalia stout, notothyrial platform thickened; brachiophores simple, blunt bosses, cardinal process a simple ridge.

#### Species assigned to *Orthambonites*

*Orthis calligramma* Dalman, 1828 (defined and described below as a basis for comparison of the many forms that have been identified as this species; *Orthambonites rotunda* Pander, 1830 and *Orthambonites lata* Pander, 1830 are regarded here as junior subjective synonyms of *O. calligramma*, and they are thus discussed further below following the description of the latter); *Orthambonites aequalis* Pander, 1830; *Orthis kreklingsensis* Öpik, 1939; *Orthambonites majusculus* Rubel, 1961; *Orthambonites fundata* Rubel, 1961; ?*Orthis novitas* Öpik, 1939.

**Remarks.** We have examined all available type material to confirm these assignments to *Orthambonites*. In his description of *O. fundata*, Rubel (1961, p. 178) mentioned only the presence of concentric fila as micro-ornamentation on the costae, but re-examination of Rubel's type material confirms that radial capillae are present both on and between the primary ribs; most of the specimens are worn and the capillae are thus not readily apparent, but where developed they closely match the pattern seen in *O. calligramma* (Pl. 1, figs 1f–g, 2f). The dorsal valve of *O.?* *novitas* resembles that of *O. kreklingsensis* except that it has a few costellae developed medially (Pl. 3, fig. 6);

the taxonomic significance of this difference is difficult to assess without the availability of a larger sample of *O. novitas*, but we provisionally include this species within *Orthambonites* and include a restricted development of costellation within our generic diagnosis. All other species assigned above to *Orthambonites* show no costellation. The long, closely adjacent ventral vascula media that characterize *Orthambonites*, and which help to distinguish the genus from others described in this paper, are particularly well illustrated in Plate 2, figure 1, and by Schuchert and Cooper (1932, pl. 2, fig. 18) and Rubel (1961, pl. 15, fig. 8).

*Occurrence.* The above group of species is restricted geographically to Baltoscandia, within a narrow time interval of the late lower Ordovician (latest Arenig to early-mid Llanvirn equivalent; Kundan Stage; uppermost *Didymograptus hirundo* to *Didymograptus bifidus* Zone; southern and central Sweden, northern Estonia, Ingria, and the Oslo region of Norway). No undoubted representatives of the genus are known from outside Baltoscandia.

*Orthambonites calligramma* (Dalman, 1828)

Plate 1, figs 1–3; Plate 2, figs 1–7; Plate 3, fig. 1

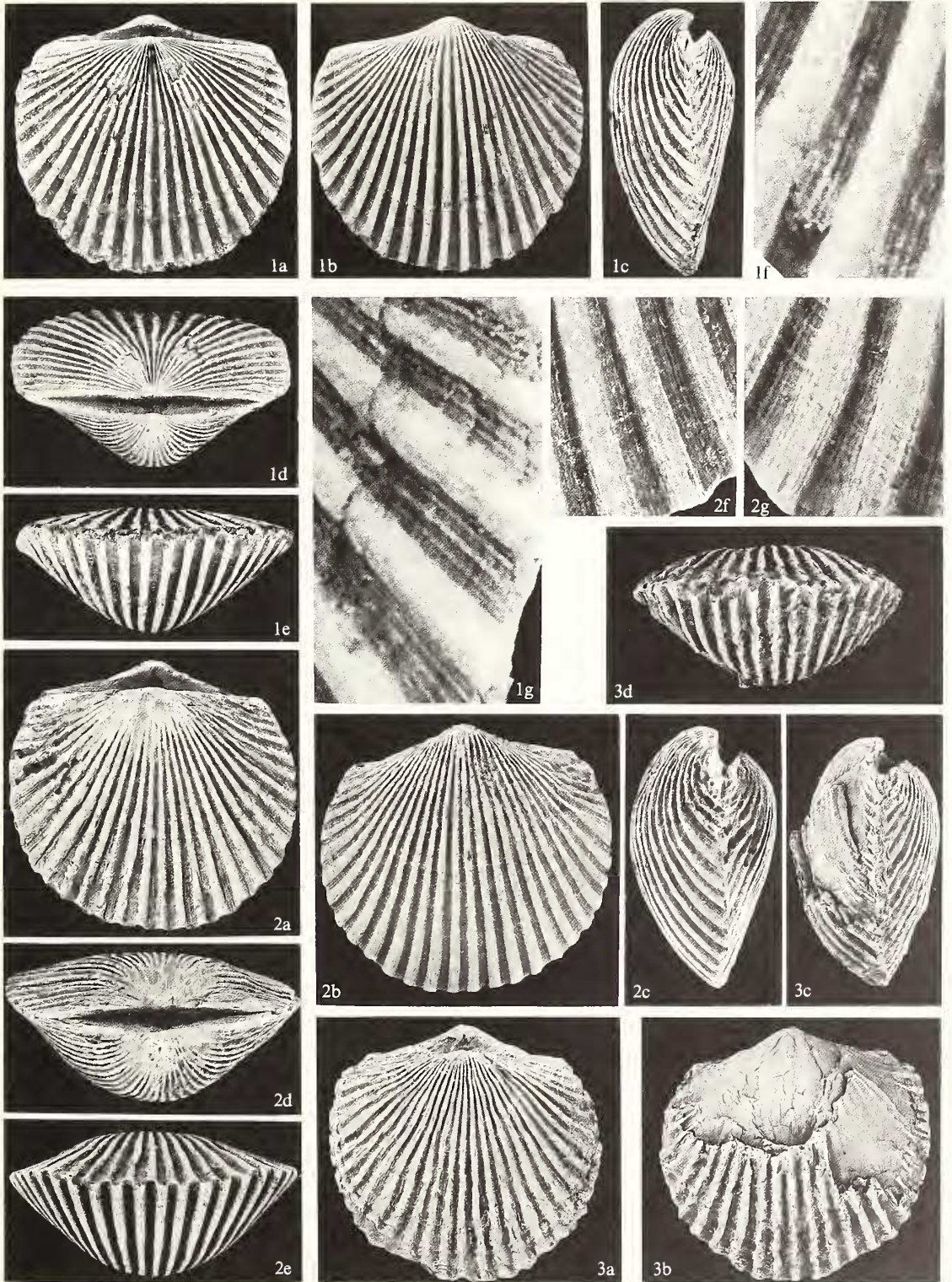
- v\*1828 *Orthis calligramma* Dalman, p. 30, pl. 2, fig. 3a–d.
- 1830 *Orthambonites rotunda* Pander, p. 82, pl. 22, fig. 6 [non fig. 5; see text above].
- 1830 *Orthambonites lata* Pander, p. 82, pl. 22, fig. 7a–d.
- v.1837 *Orthis calligramma* Dalman; Hisinger, p. 71, pl. 20, fig. 10a–c.
- 1932 *Orthis* cf. *calligramma* Dalman; Schuchert and Cooper, pl. 2, figs 7, 9, 11, 13.
- ?1932 *Orthis rotunda* (Pander); Schuchert and Cooper, pl. 2, figs 10, 16, 18.
- v.1953 *Orthis calligramma* Dalman; Alikhova, p. 30, pl. 2, figs 1–5.
- v.1960 *Orthis calligramma* Dalman; Alikhova in Sarycheva, pl. 9, figs 12–14.
- v.1961 *Orthambonites calligramma* (Dalman); Rubel, p. 177 pars [non pl. 15, fig. 1].
- v.1965 *Orthambonites calligramma* (Dalman); Williams in Williams *et al.*, fig. 196: 4a–e.
- non 1985 *Orthis calligramma* Dalman; Cocks, p. 56, pl. 5, fig. 2.2A–C [= *O. callactis* Dalman, 1828]

*Holotype* (by monotypy). RM Br102501, conjoined valves, figured Pl. 1 fig. 2a–g; from Skarpåsen, Östergötland, Sweden; almost certainly from the lower part of the zone of *Asaphus* (*Asaphus*) *raniceps* ('Raniceps Limestone'), topmost lower Ordovician (Kundan Stage, lower Valastean Substage, lower *D. bifidus* Zone); the original specimen collected by Olivecrona and figured both by Dalman and Hisinger (see synonymy). Dalman's description (1828, p. 30) appears to refer to a single specimen and in the absence of evidence to the contrary we thus consider that this is the holotype rather than a lectotype.

*Material.* The species is not particularly common in the topotype area in Östergötland and specimens from there are normally not well preserved; the Stockholm collections from this region are mostly from localities at Borghamn and Husbyfjöl. Our description is based in addition on samples from the lower part of Valastean age beds on northern Öland, and particularly on well-preserved specimens from sections at Hälludden and Hagudden (e.g. RM Br106189–Br106195). The

EXPLANATION OF PLATE I

Figs 1–3. *Orthambonites calligramma* (Dalman, 1828). 1a–g, neotype of *Orthambonites rotunda* Pander, 1830; RM Br66169; Voka Beds, Kundan Stage, lower Valastean Substage (B<sub>III</sub>β); Pulkova, Ingria, Russia; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with details of capillate ornament on left anterolateral and right anterolateral flanks of dorsal valve; a–e × 2, f–g × 10. 2a–g, holotype; RM Br102501; figured Dalman 1828, pl. 2, fig. 3a–d and Hisinger 1837, pl. 20, fig. 10a–c; probably from the Raniceps Limestone, Kundan Stage, lower Valastean Substage; Skarpåsen, Östergötland, Sweden; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with details of fine capillae and fila on right anterolateral and left anterolateral flanks of ventral valve; a–e × 2, f × 8, g × 10. 3a–d, RM Br106189; lower Raniceps Limestone, Kundan Stage, lower Valastean Substage; Hagudden (level +45 +20D), Öland, Sweden; dorsal, ventral, lateral and anterior views of conjoined valves, × 2.



range of *O. calligramma* at Hälludden was shown by Jaanusson and Mutvei (1982, fig. 7). The contemporaneous specimens described by Alikhova (1953) and Rubel (1961) from Ingria have also been examined, together with smaller samples from Pulkova in Ingria and from Tsitre in northern Estonia.

*Description.* Initially ventribiconvex, mature shells subequally biconvex to only slightly ventribiconvex, with uniform transverse and longitudinal curvature or with dorsal valve flattening slightly peripherally, maximum depth 52–67 per cent of maximum width in three mature shells. Subcircular at maturity, some juvenile dorsal valves approaching subtriangular, 95 per cent as long as wide (OR 91.1–96.6;  $n = 4$ ), dorsal valve about 90 per cent as long as ventral valve. Cardinal angles obtuse to rounded, hinge width 76–97 per cent (mean 84 per cent;  $n = 4$ ) of maximum width, which is close to the mid-length. Lateral and anterior margins evenly curved, commissures crenulate, anterior commissure rectimarginate or very weakly deflexed ventrally in peripherally flattened shells. Umbones low, inconspicuous, ventral beak suberect, not curved over the hinge line. Ventral interarea short, gently concave, weakly apsacline, delthyrium open with a rounded apex, delthyrial angle from about 50° to 75°. Dorsal interarea plane, anacline, notothyrium open.

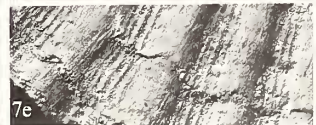
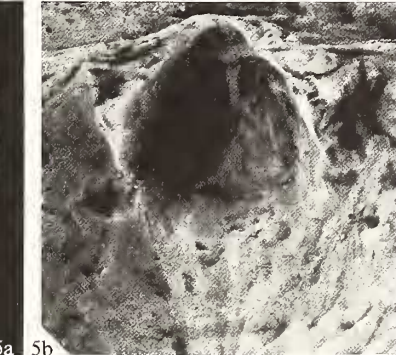
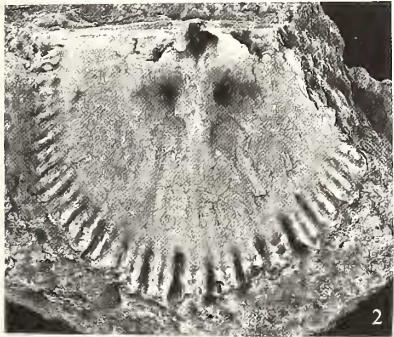
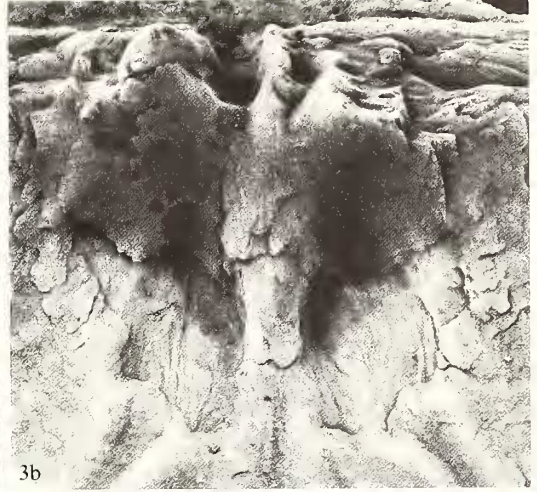
Ornament costate and capillate, ribs initially relatively slender, rounded, 11 in a 10 mm arc at the 10 mm growth stage of the dorsal valve, widening gradually anteriorly to become subrounded to subflattened at the anterior margin of mature shells. Commonly 30–32 ribs on mature dorsal valves (OR 29–37). The costae are straight with an amplitude close to 0.5 mm and a wavelength anteriorly of up to 2 mm, interspaces and ribs of subequal width. In the available material there is only one example of a rib originating outside the umbonal area, arising on the flanks of a costa at the 2.5 mm growth stage. Both costae and interspaces bear slender, rounded capillae with a mean spacing of 4 to 5 per mm (Pl. 1, figs 1f–g, 2f), though they are commonly worn on the rib crests. Growth lines normally weak to inconspicuous, but very fine, slightly lamellose fila are present over the whole surface (Pl. 1, fig. 2g).

Delthyrial cavity large and deep, with a thick, concave pedicle collar lining about half the height of the posterior wall. The collar is buttressed anteriorly by a subflattened, tapering median septum that extends anteriorly for about 30 per cent of the length of the delthyrial cavity. Teeth relatively large, deltidodont, bluntly rounded in outline, supported by thick, suberect dental plates; lateral cavities shallow. Muscle field deeply impressed, subpentagonal, extending anteriorly beyond the delthyrial cavity for about 30% of the valve length, widest at the base of the dental plates (25 per cent of maximum valve width) then tapering anteriorly to a straight anterior margin. Anterior to the dental plates the muscle field is unbounded by ridges, but is confined within a hollow defined by swollen, rounded margins. Diductor scars large, oval, divided posteriorly by the median ridge, adductor scars not clearly preserved on the material available but probably confined to a small area immediately anterior to the ridge. Across its full width the anterior margin of the muscle field merges smoothly into a broad, slightly raised ridge of shell that tapers anteriorly to about the mid-length of the valve and is grooved along its mid length; the raised lateral areas of the ridge represent the inner margins of thick vascular media of a saccate mantle canal system. From the anterior margin of the muscle field the vascula media extend anteriorly beyond the median ridge as long, closely adjacent, parallel, straight to slightly

#### EXPLANATION OF PLATE 2

Figs 1–7. *Orthambonites calligramma* (Dalman, 1828). 1, RM Br20218; lower Raniceps Limestone, Kundan Stage, lower Valasteian Substage; Hälludden, northern Öland, Sweden; mould of interior of exfoliated ventral valve showing long, parallel, proximally adjacent vascula media,  $\times 2$ . 2, RM Br106191; horizon and locality as for fig. 1; interior of dorsal valve,  $\times 2$ . 3a–b, RM Br106190; horizon and locality as for fig. 1, level +41 +46D; interior of dorsal valve ( $\times 2$ ) and oblique-anterior detail of cardinalia showing the thickened brachiophores and notothyrial platform ( $\times 6$ ). 4a–b, RM Br106192; horizon and locality as for fig. 1; interior of dorsal valve ( $\times 2$ ) and oblique-lateral detail of cardinalia ( $\times 4$ ; right hand brachiophore broken away). 5a–b, RM Br106193; horizon and locality as for fig. 1; loose in section; interior of ventral valve ( $\times 2$ ) and oblique-anterior detail of delthyrial chamber showing the distinctive pedicle collar. 6, CNIGR 21/7135; figured Alikhova 1953, pl. 2, fig. 5; Kundan Stage; Volkhov River between Obukhovo and Simonkovo, Ingria, Russia; interior of dorsal valve,  $\times 2$ . 7a–e, CNIGR 17/7135; figured Alikhova 1953, pl. 2, fig. 1a–e; horizon and locality as for fig. 6; dorsal, ventral, lateral and anterior views of conjoined valves ( $\times 1.5$ ), with detail of capillate ornament on left anterolateral flank of dorsal valve ( $\times 5$ ).





arcuate tracks that reach to well over 80 per cent of the valve length, curving laterally and then posteriorly only close to the anterior margin around the crenulated rim formed by the impress of the external ribbing (Pl. 2, fig. 1).

*Cardinalia robusta*, increasingly thickened with growth, raised on a stout notothyrial platform that occupies up to 25 per cent of the valve length and merges smoothly anteriorly with a broad, swollen, longitudinal median ridge that decreases gradually in height to the anterior margin of the muscle field just posterior to the mid-length of the valve; the ridge occupies up to about 13 per cent of the valve width and may be weakly carinate along its length, though it is usually rounded by secondary shell in mature individuals, and anteriorly it may pass into a broad, shallow groove. Notothyrial cavity broad and deep, cardinal process a simple, thick ridge with a rounded to subcarinate cross-section, produced anteriorly to merge smoothly with the posterior end of the median ridge. The deep muscle attachment hollows adjacent to the cardinal process may each be divided in two by a transverse, rounded ridge. Brachiophores thick, grooved along inner faces, sub-erect or with tops convergent relative to bases, divergent anterolaterally at about 100–120° to one another, originally bluntly triangular distally but becoming increasingly thickened and rounded with growth, with thick bases that swell out from the notothyrial platform and median ridge. Sockets large, suboval with well rounded floors. Dorsal muscle field deep, occupying about 30–37 per cent of valve width and 50 per cent of the length, bisected longitudinally throughout by the median ridge. Posterior scars set in deep, rounded hollows excavated partly below the notothyrial platform, separated from the smaller and less deeply impressed anterior pair in some specimens by short, transverse swellings from the median ridge. Vascular system apocopate, with broad, well impressed *vascula media* diverging anterolaterally from the centre of the anterior margin of the adductor muscle scars.

The internal periphery of both valves is crenulated strongly by broad, flat ridges with a shallow central groove, separated by deep, narrow, rounded intergrooves.

#### *Dimensions of figured specimens*

	Maximum length ventral valve	Maximum length dorsal valve	Maximum width	Hinge width	Maximum thickness	Maximum number of ribs along commissure
RM Br102501, conjoined valves (Holotype)	21.3	19.2	22.5	17.2	11.9	31
RM Br106189, conjoined valves	20.3	18.6	21.0	16.4 (est.)	11.4	31

#### EXPLANATION OF PLATE 3

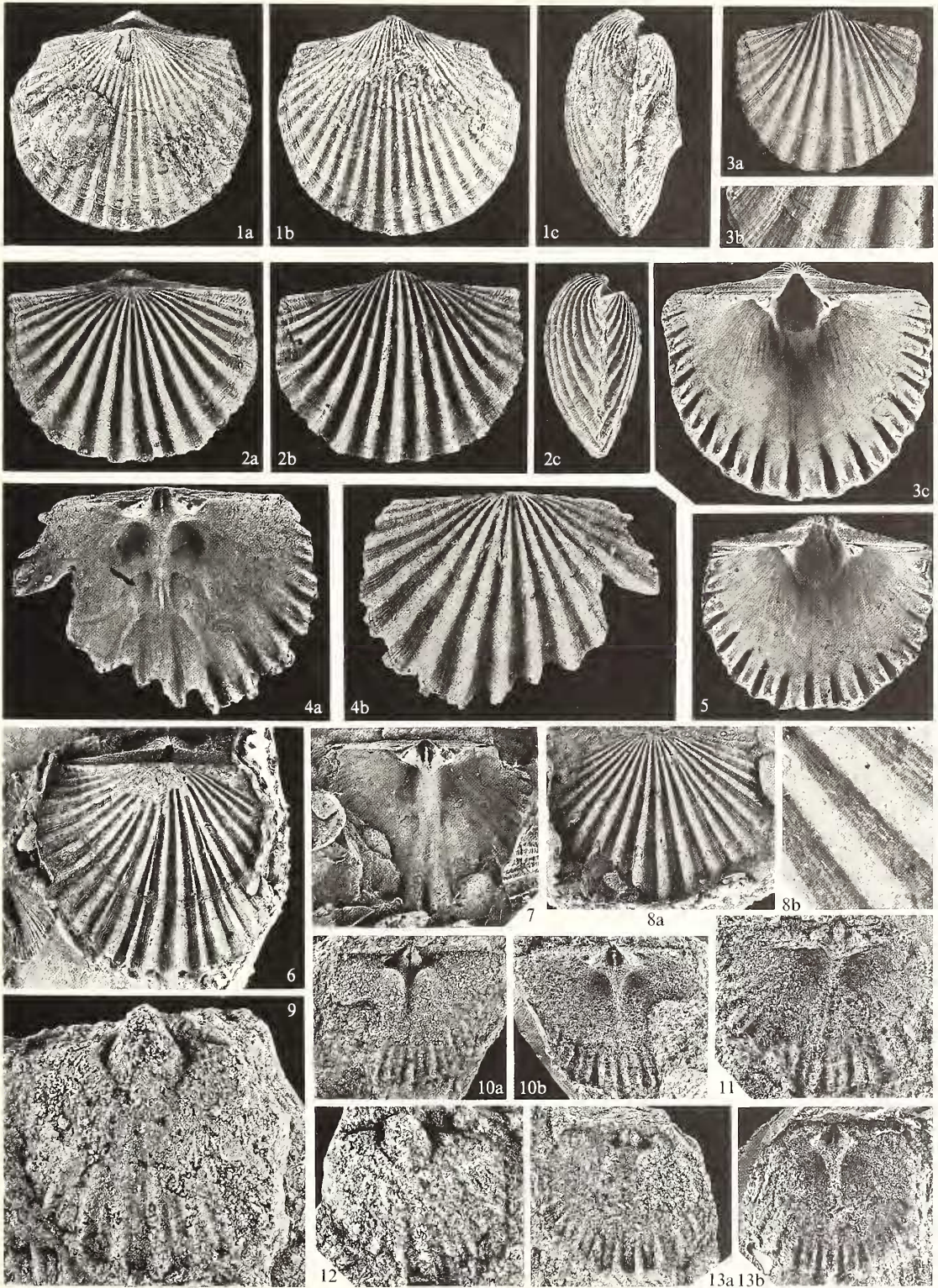
Fig. 1. *Orthambonites calligramma* (Dalman, 1828). 1a–c, RM Br134535; Voka Beds, Kundan Stage, lower Valasteian Substage ( $B_{III\beta}$ ); Tsitre, Estonia; dorsal, ventral and lateral views of conjoined valves,  $\times 2$ .

Figs 2–5. *Orthambonites* sp. All from Vokhovian Stage ( $B_{IV}$ ); Volkhov, Izvos, Ingria, Russia. 2a–c, RM Br116438; dorsal, ventral and lateral views of conjoined valves,  $\times 2$ . 3a–c, RM Br116434; exterior of ventral valve ( $\times 2$ ), detail of capillate ornament on left anterolateral flank ( $\times 5$ ), and interior of valve ( $\times 3$ ). 4a–b, RM Br116435; interior and exterior of dorsal valve,  $\times 3$ . 5, RM Br116429; interior of ventral valve showing proximally adjacent *vascula media*,  $\times 2$ .

Fig. 6. *Orthambonites? novitas* (Öpik, 1939). Holotype; PMO 2338; figured Öpik 1939, pl. 5, fig. 5; Expansus Shale ( $3c\beta$ ; Arenig); Rokstadåsen, Hedenstad, Oslo Region, Norway; latex cast of mould of dorsal valve and ventral interarea,  $\times 2.5$ .

Figs 7–8. *Orthambonites kreklingensis* (Öpik, 1939). 7, holotype; PMO 61090b; figured Öpik 1939, pl. 1, fig. 1; horizon as for fig. 6; Krekling, Oslo Region, Norway; latex cast of interior of dorsal valve;  $\times 3$ . 8a–b, PMO 61090a; horizon and locality as for Fig. 7; latex cast of exterior of dorsal valve ( $\times 2$ ) and detail of capillate ornament on right anterolateral flank ( $\times 5$ ).

Figs 9–13. *Paralenorthis proava* (Salter, 1866). All from Carmel Formation, Arenig Series; coarse sandstones in low scarp 90 m north-east of ruined cottage, Prys-Owain-Bach, Carmel, 2 km south-west of Llanerchymedd on B5112 road, Anglesey, north Wales. SH 3986 8282. 9, NMW 88.17G.1; internal mould of ventral valve,  $\times 3$ . 10a–b, NMW 88.17G.2; internal mould of dorsal valve and latex cast,  $\times 2$ . 11, NMW 88.17G.3; latex cast of internal mould of dorsal valve,  $\times 2$ . 12, NMW 88.17G.4; internal mould of ventral valve,  $\times 2$ . 13a–b, NMW 88.17G.5; internal mould of dorsal valve and latex cast,  $\times 2$ .



JAANUSSON and BASSETT, *Orthambonites*, *Paralenorthis*

RM Br106193, ventral valve	20.6	—	22.6	—	7.4	> 33
RM Br106190, dorsal valve	—	18.8	—	22.0 (est.)	—	—
RM Br106191, dorsal valve	—	19.2	22.5	21.8 (est.)	—	—
RM Br106192, dorsal valve	—	15.8	16.9	14.1	—	—
RM Br20218, internal mould of ventral valve	30.5	—	32.9	—	—	—
RM Br134535, conjoined valves	23.2	20.9	24.6	20.5 (est.)	11.3	29
RM Br66169, conjoined valves [= Neotype of <i>O. rotunda</i> ]	20.5	18.8	21.3	17.7	9.9	30
CNIGR 17/7135, conjoined valves	24.0	21.9	25.7	20.5	19.1	30
CNIGR 21/7135, dorsal valve	—	15.8	18.2	13.0	9.9	32

*Occurrence.* Despite being recorded from many areas and stratigraphical levels throughout the world, *O. calligramma* is known with certainty only from the lower Valastean Substage of the Kundan Stage in Sweden, northern Estonia, and Ingria.

*Comparison.* *O. fundata* and *O. majuscula* are approximately contemporaneous species in different facies of Valastean beds at a slightly higher lithostratigraphical level than that at which *O. calligramma* occurs. *O. fundata* from the Pakri Sandstone has only 22–26 primary ribs and a weakly to moderately convex dorsal valve, contrasting with the relatively strong dorsal curvature of *O. calligramma* in which typical populations have 30–32 primary ribs as a mean, and in which only one specimen that we have examined has fewer than 30 ribs (29). *O. majuscula* also differs from *O. calligramma* in its weak dorsal convexity and in having fewer primary ribs; in the latter respect, Rubel (1961, p. 175) reported a range of 20 to 33 ribs in *majuscula*, but examination of the type series (by M. G. B.) shows that 22 or 23 is the most common figure (23 on the dorsal valve of the holotype). The higher number of ribs in some larger specimens suggests some overlap with *O. calligramma*, but apart from the differences in convexity, *majuscula* also differs in having somewhat flatter costae, smaller, less robust teeth, only a very weak ridge anterior to the ventral muscle field, and a cardinal process that is swollen at its mid length. Both *majuscula* and *fundata* have the radial and concentric micro-ornament typical of *calligramma*, and both have the long, subparallel ventral vascula media and stout brachiophores diagnostic of the genus. *O. kreklingsensis* and *O. novitas* are both readily separable from *O. calligramma* by their weaker dorsal convexity and more slender ribbing, and as noted above (p. 25), *novitas* also differs in having costellae developed medially.

Rubel (1961, p. 177, fig. 9) examined the variation in number of ribs in *Orthambonites* specimens through successive stratigraphical levels in the Kundan of the Volkhov river section in Ingria, ranging from the base of the Valastean Substage to the lower part of the Aluojan Substage; he interpreted the pattern as variation within a single species, *O. calligramma*, showing upward decrease in rib numbers from 30–34 in the lower Valastean to 19–22 in the uppermost Valastean to lower Aluojan. No specimens were recorded with 23–24 or 27–29 ribs, and our comparison of Ingrian specimens in the Stockholm collections also suggests that the variation is discontinuous; unfortunately these latter collections lack stratigraphical control. Swedish specimens of *O. calligramma* from lower Valastean beds mostly have 31–33 ribs (OR 29–34), matching closely with Rubel's material from the same level in Ingria, and since there are no consistent differences in other morphological features these forms are considered to be conspecific (note that the full range of our Ingrian collections assigned to *calligramma* is 29–37 ribs). Ingrian specimens with 25–26 ribs from the middle part of the Valastean Substage may be a separate species; in rib number, outline and

convexity they resemble Pander's figure of *Orthambonites aequalis* Pander, 1830, pl. 22, fig. 5 (but not fig. 6, see p. 23). Rubel's forms with only 19–22 ribs at the top of his section are present in our collections, and they might again represent a separate species. However, in order to define the differences between these forms more precisely a statistical study would be required, for which adequate collections are not available.

*Remarks.* We have commented above on the likely synonymy of *O. calligramma* and *O. rotunda*, which we base on the close similarity in outline, convexity, attitude and relative lengths of the interareas, and number of ribs. From a study of the original description and illustrations we also consider that *O. lata* Pander, 1830, p. 82, pl. 22, fig. 7 is a probable synonym of *O. calligramma*. Alikhova (1953, p. 30) also synonymized these three species (note that her inclusion of Pander's name *aequalis* is a reference to the original figure, which as we have noted above on pp. 23–24 was transposed with that of *rotunda*).

L. E. Popov (VSEGEI, St Petersburg) has confirmed for us that the whereabouts of all the specimens used by Pander for his 1830 monograph have been unknown for over a century, and that they must be regarded as lost. In view of our recommendation and pending application to the ICZN to recognize *O. rotunda* as the formal type species of *Orthambonites*, it is desirable to stabilize the specific name by designation of a neotype. We here designate RM Br66169 accordingly; it is from Pulkova, Ingria, and some limonitic ooids in the adhering matrix indicate that it is from the Voka Beds (Kundan Stage, lower Valastean Substage; Pl. 1, fig. 1a–g). In outline, convexity, and rib number (30) this specimen matches Pander's original illustration and description in close detail; it is also from one of the sections described by Pander in his original study area. The presence of this form in the Voka Beds of Ingria reinforces the view that it is a junior synonym of *O. calligramma*, as this is the level from where Rubel (1961, fig. 9, lowest part of graph) recorded what we take to be typical specimens of *calligramma*.

In searching for Pander's original material in St Petersburg, L. E. Popov discovered some collections now housed in the Palaeontological Museum of the Institute of Technical Geology (Gorny Institut), and these were studied by M.G.B. in 1983. The specimens were probably not collected by Pander himself, but most likely he obtained them as late as the 1850s from P. Jeremeyev, a State Captain in the Engineering Corps of the Russian Army; included are brachiopods from well known localities in Ingria, including Popovka and Izvos, and the associations suggest that they are mostly from the Volkhovian, Kundan, and Aserian stages. Although not the type material, these collections have some relevance to Pander's own concept of *Orthambonites* and to the possible synonymy of *O. rotunda* and *O. calligramma*. Among the orthacean brachiopods present are specimens of *Orthambonites*, *Nicolella*, *Orthis*, *Glossorthis*?, and *Cyrtanotella*. All the *Orthambonites* specimens are named as *Orthis calligramma* and they were probably identified and named as such by Pander himself (L. E. Popov pers. comm.); in a number of cases some of the other genera are also included within samples identified as *calligramma*. The evidence from these collections suggests that at that time Pander probably believed all his *Orthambonites* species to be synonyms of *O. calligramma*. Suppression of *O. transversa* as the formal type species of the genus, and even the possible synonymy of *O. rotunda* with *O. calligramma* does not therefore alter the concept of the genus as seen subsequently by Pander himself.

#### Genus PARALENORTHIS Havlíček and Branisa, 1980

*Type species.* *Paralenorthis immitatrix* Havlíček and Branisa, 1980; from un-named upper Arenig or Llanvirn beds of San Lucas, Bolivia.

*Diagnosis.* Subequally biconvex with only moderate curvature, ventral valve slightly carinate, dorsal valve weakly sulcate, shells comparatively small, ventral interarea apsacline. Ornament costate or rarely sparsely costellate, and capillate. Ventral muscle field extending anteriorly only slightly

beyond the delthyrial cavity, anterior margin rounded or faintly lobate; ventral vascula media diverge immediately in front of the muscle field. Cardinal process a simple ridge, brachiophores blunt bosses.

*Nomenclatorial history of the genus.* Andreeva (*in* Andreeva and Nikiforova 1955) erected *Leuorthis* based on material from the middle Ordovician of the Siberian Platform, but reported subsequently (Nikiforova and Andreeva 1961, p. 73) that the type species of *Leuorthis*, *L. girardi*, had been based by mistake on a combination of a ventral valve of a *Miuella* species and a dorsal valve of a *Hesperorthis*. As based on the lectotype of the type species (designated subsequently by Havlíček and Branisa 1980, p. 16), *Leuorthis* is a junior subjective synonym of *Hesperorthis*. Unfortunately the taxonomic status of *Leuorthis* as corrected by Nikiforova and Andreeva (1961) escaped the attention of many brachiopod specialists for a number of years.

Williams (*in* Williams *et al.* 1965, p. H311) redefined *Leuorthis* for *Orthambouites*-like forms with ventral vascula media that diverge from immediately in front of the muscle field. It should be noted that the species used by him to illustrate the genus – *L. mostellerensis* (Cooper, 1956) – is included in this paper (p. 38) in our new genus *Sulevorthis*. Williams's concept of *Leuorthis* was used subsequently by several writers (e.g. Bates 1968, 1969; Williams 1974). Because *Leuorthis* is not now available for this group of species (see also Neuman and Bates 1978, p. 588), Havlíček and Branisa (1980) established *Paraleuorthis* as a replacement for *Leuorthis* in the sense of Williams (*in* Williams *et al.* 1965), with a type species from Bolivia.

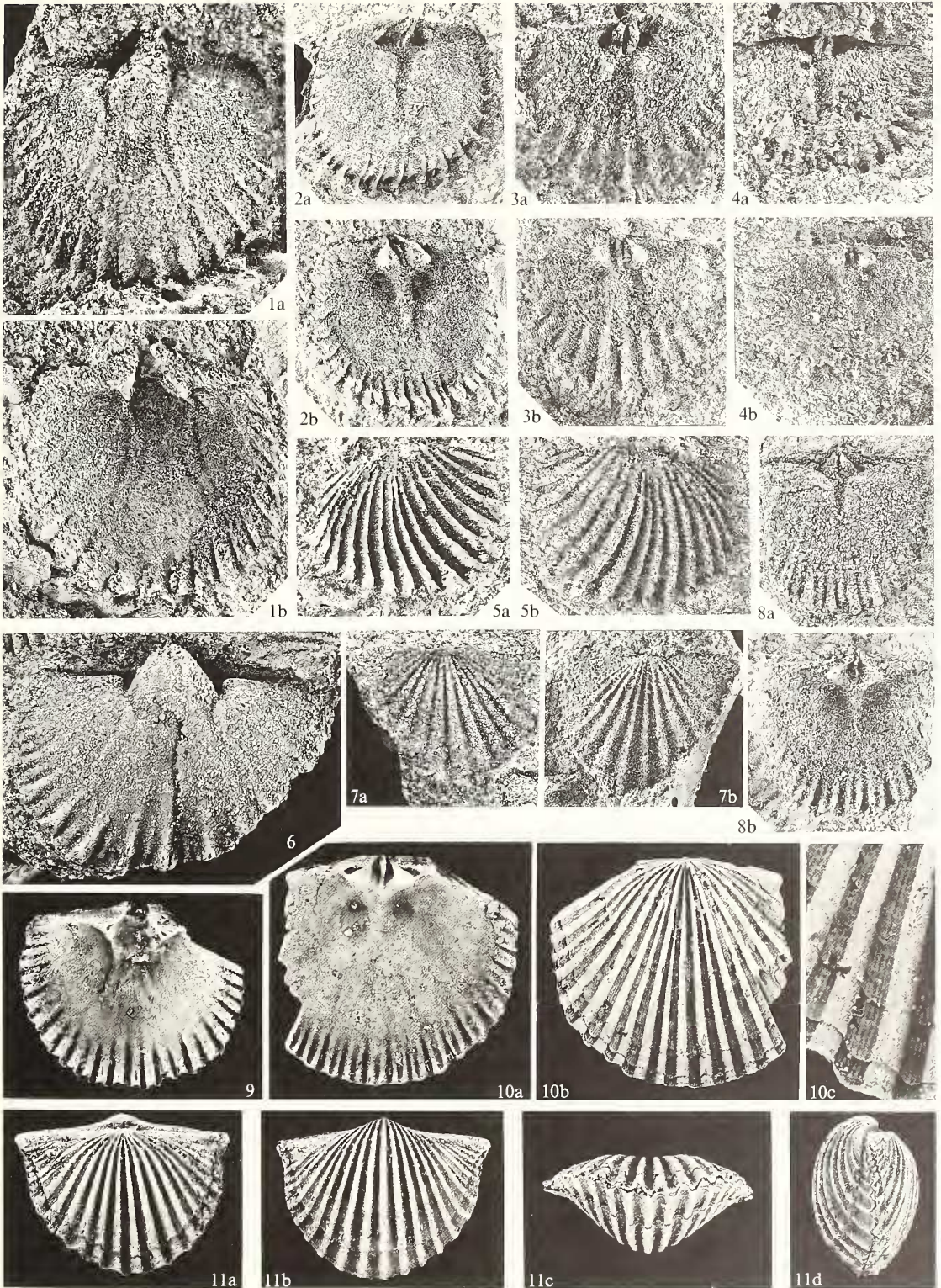
Our survey of *Orthambouites*-like genera reveals that a number of species groups have ventral vascular media which diverge widely from their proximal extremities close to the anterior margin of the muscle field; for example, in addition to *Paraleuorthis* this feature is typical of *Sulevorthis* gen. nov. and may also be a constant characteristic of *Shoshouorthis* gen. nov. In redefining *Paraleuorthis* therefore we recognize a combination of characters, of which the nature of the ventral vascula media is just one; the divergent pattern referred to above does appear to be useful consistently as a contrast from the long, subparallel tracks of *Orthambouites*.

#### *Species assigned to Paraleuorthis*

*Paraleuorthis immitatrix* Havlíček and Branisa, 1980; *Productus orbicularis* Pander, 1830; *Spirifer alatus* J. de C. Sowerby *in* Murchison, 1839; *Orthis calligramma* var. *proava* Salter, 1866; *Orthis panderiana* Hall and Clarke, 1892; *Orthis calligramma* var. *serica* Martelli, 1901 [*Orthis calligramma* var. *chinensis* Chang, 1934 and

#### EXPLANATION OF PLATE 4

- Figs 1–5. *Paraleuorthis robusta* (Neuman, 1964). All from R. B. Neuman syntype collection; Shin Brook Formation, Whiterock Series; falls in Crommet Brook, Penobscot County, Shin Pond quadrangle, north-eastern Maine, USA (USGS locality CO-3608; locality E of Neuman 1964, p. E12). 1*a–b*, USNM 423930*a*; internal mould of ventral valve and latex cast, showing posteriorly separated and divergent vascula media,  $\times 3$ . 2*a–b*, USNM 423933*a*; internal mould of dorsal valve and latex cast,  $\times 2$ . 3*a–b*, USNM 423932; internal mould of dorsal valve and latex cast,  $\times 2$ . 4*a–b*, USNM 423931*a*; internal mould of dorsal valve and latex cast,  $\times 2$ . 5*a–b*, USNM 423931*b*; external mould of ventral valve and latex cast,  $\times 2$ .
- Figs 6–8. *Paraleuorthis proava* (Salter, 1866). All from Carmel Formation, Arenig Series; coarse sandstones in low scarp 90 m north-east of ruined cottage, Prys-Owain-Bach, Carmel, 2 km south-west of Llanerchymedd on B5112 road, Anglesey, north Wales, SH 3986 8282. 6, NMW 88.17G.6*a*; internal mould of ventral valve showing posteriorly separated and divergent vascula media,  $\times 3$ . 7*a–b*, NMW 88.17G.6*b*; external mould of dorsal valve and latex cast,  $\times 2$ . 8*a–b*, NMW 88.17G.6*c*; internal mould of dorsal valve and latex cast,  $\times 2$ .
- Figs 9–11. *Paraleuorthis orbicularis* (Pander, 1830). All from Volkhovian Stage; Izvos, Ingria, Russia. 9, RM Br73924; interior of ventral valve showing posteriorly separated and divergent vascula media,  $\times 3$ . 10*a–c*, RM Br73923; interior and exterior of dorsal valve ( $\times 3$ ) and detail of capillate ornament on left posterolateral flank ( $\times 10$ ). 11*a–d*, RM Br73922; dorsal, ventral, anterior and lateral views of conjoined valves,  $\times 3$ .



*O. calligramma* var. *hupehensis* Chang, 1934 were regarded by Xu and Liu (1984, p. 68) as synonyms of *P. serica*]; *Orthis marshalli* Wilson, 1926; *Orthis buttsi* Schuchert and Cooper, 1932 [pro *O. crassica* Butts, 1926 non *Orthambonites crassica* Pander, 1830]; ?*Orthis minusculus* Phleger, 1933; *Orthis alabamensis* Ulrich and Cooper, 1938; ?*Orthambonites angulatus* Cooper, 1956; *Orthambonites robustus* Neuman, 1964; *Orthambonites riojanus* Levy and Nullo, 1973; *Orthambonites mollesensis* Levy and Nullo, 1973.

*Discussion.* Of the above fourteen species assigned to *Paralenorthis*, four were recorded by Williams (1974, p. 53) as *Lenorthis* (*P. orbicularis*, *P. alata*, *P. proava*, and *P. pauderiana*). Two further species (*P. inimitatrix* and *P. marshalli*) were included in *Paralenorthis* by Havlíček and Branisa (1980). The other species referred to *Lenorthis* or *Paralenorthis* in these two papers are here assigned to *Sulevorthis* gen. nov. According to Ross (1970, p. 54), *Orthis subalata* Ulrich and Cooper, 1938, is a junior subjective synonym of *P. marshalli* Wilson, 1926.

Specimens in which the ventral vascula media are divergent from their proximal ends are known in *Paralenorthis orbicularis* (Pl. 4, fig. 9), *P. alata* (Bates 1969, pl. 3, fig. 3; pl. 5, figs 3, 5), *P. proava* (Bates 1968, pl. 2, figs 3, 6; Pl. 4, fig. 6; cf. Williams 1974, pl. 8, fig. 2), *P. marshalli* (Ross 1970, pl. 3, fig. 9), *P. angulata* (Cooper 1956, pl. 36, fig. 20), *P. robusta* (Neuman 1964, pl. 1, figs 1, 3, 5; Pl. 4, figs 1a–b herein), *P. inimitatrix* (Havlíček and Branisa 1980, pl. 1, figs 2, 4) and *P. mollesensis* (Levy and Nullo 1973, pl. 1, figs 11–19).

Levy and Nullo (1973) compared one of their new species ('*Orthambonites*' *riojanus*) from the Molles Formation in the Famatina Range of the Argentinian Precordillera with one North American species that we assign here to *Paralenorthis* (*P. buttsi*), and a second that we assign (see p. 38) to *Sulevorthis* (*S. blomtensis*). They also compared their second species ('*O.*' *mollesensis*) with a North American species assigned here to *Sulevorthis* (*S. rotundiformis*). Although we have not examined the Argentinian specimens we consider that the descriptions and illustrations of both *riojanus* and *mollesensis* suggest an assignment to *Paralenorthis*, particularly in features of ornament, convexity, attitude of interareas, musculature, and nature of the ventral vascula media. The vascular pattern in Argentinian material was well illustrated originally by Kayser (as *calligramma*) as long ago as 1876 (pl. 3, fig. 18a). It is not unlikely that the two nominal species are conspecific. They are from the same Formation and locality and the described minor differences may be due to state of preservation. Minor variation in the described number of costae (18 in *riojanus* and 14–17 in *mollesensis*) is well within the range observed in other species of *Paralenorthis*. According to Levy and Nullo (1973, p. 140), the Molles Formation is of late Llanvirn to early Llandeilo age; other assessments suggest that the late Llanvirn correlation is most likely (e.g. Turner 1960, p. 96; Cuerda 1973, p. 285; Aceñolaza 1976, p. 483).

Martelli's (1901) original illustrations of '*Orthis*' *serica* from Hanzhong in southern Shaanxi Province, China, do not show the nature of the vascularia, but we assign this species to *Paralenorthis* on the assumption that specimens described and illustrated under the same name by Li *et al.* (1975, p. 103, text-fig. 51, pl. 11, figs 1–4) from the Xiliangsi Formation in the same general region are conspecific; in these specimens the ventral vascula media diverge laterally before the mid length of the shell, and in other details of convexity, ornament, attitude of interareas, and internal morphology the material conforms closely with *Paralenorthis*. Examination (by M.G.B.) of similar specimens from Guizhou Province identified as *O. serica* also confirms the general features of the genus and a close similarity with the British *O. proava*, although in the Guizhou collections the vascular tracks were again not preserved. In the other species included here within the genus the course of the main ventral vascular tracks has also not been observed because of poor preservation, so that generic assignment is only provisional on the basis of overall morphological similarity.

Micro-ornament is not always preserved in silicified specimens and in those embedded in coarse clastic matrix. In *Paralenorthis*, radial capillae have been observed in *P. orbicularis*, *P. alata*, *P. cf. proava* (Williams 1974, pl. 8, fig. 3), *P. pauderiana*, *P. serica*, *P. buttsi*, *P. alabamensis* (traces, personal observations), and *P. inimitatrix*.

The Baltoscandian *P. orbicularis* differs somewhat from other species assigned to the genus in having a shorter ventral interarea (Pl. 4, fig. 11d; Rubel 1961, pl. 14, figs 7, 11), a relatively more



strongly convex dorsal valve, and shorter cardinalia and ventral muscle field. This species is provisionally retained in the genus because in several species of *Paralenorthis* the available information on relative valve convexities and interarea length and attitude is insufficient for further taxonomic discrimination.

*Paralenorthis* differs from *Orthambonites* in normally having a smaller adult shell (known maximum length of *Paralenorthis* is 18 mm; *Orthambonites* is consistently a relatively large genus, with a known maximum length up to 33 mm), a more distinctly sulcate dorsal valve, a somewhat carinate ventral valve, longer ventral interarea, and ventral vascula media that diverge anterolaterally from their proximal extremities. *Sivorthis* has proximally parallel ventral vascula media, is more finely ribbed, and the brachiophores appear to have a more elaborate morphology.

*Occurrence.* The above species are distributed widely through strata of mid lower to mid middle Ordovician age (*Didymograptus extensus* to *Glyptograptus teretiusculus* Zones):

**SOUTH AMERICA:** Bolivia, un-named upper Arenig or Llanvirn beds (*P. inunitatrix* and *P. cf. alata*; Havlíček and Branisa 1980). Argentina, Precordillera, Famatina Range, Molles Formation of Famatina Group, probably upper Llanvirn (*P. riojanns* and *P. mollesensis*; Levy and Nullo 1973).

**NORTH AMERICA:** Northern Appalachians, Maine, Shin Brook Formation, Whiterock (*P. robusta*; Neuman 1964). Southern Appalachians, Blount belt, *G. teretiusculus* equivalents, Tennessee, Arline Formation (*P. angulata*; Cooper 1956) and Alabama, Little Oak Formation (*P. buttsi*; Cooper 1956); Southern Appalachians, Alabama, Odenville Limestone, upper Ibexian (*P. alabamensis*; Ulrich and Cooper 1938). Quebec, Canada, limestone boulders in Levis Shale and Solomons Corners Formation, upper Ibexian (*P. pandariana*; Ulrich and Cooper 1938). British Columbia, Canada, Skoki Formation, Whiterock (*P. marshalli*; Wilson 1926; see also Ross 1970, p. 55). Great Basin of western USA, Nevada and California, Antelope Valley Formation, Whiterock (*P. marshalli* and *P. ? minusculus*; Ross 1970); Utah, Juab Limestone, basal Kanosh Shale and dolomite equivalent of Swan Peak Quartzite, Whiterock (*P. subalata* [= *P. marshalli*]; Ulrich and Cooper 1938; Jensen 1967, p. 89).

**CHINA:** Hanzhong, southern Shaanxi Province, Siliangssu [Xiliangsi] Formation, Arenig equivalent above *D. protobifidus* and *D. cf. deflexus* faunas (*P. serica*; Martelli 1901; see also Li *et al.* 1975, p. 103; also Yang and Wang 1955, p. 125, pl. 66, figs 11, 14–17, 21; Wang *et al.* 1964, p. 91, pl. 9, figs 16–22); western Hupeh Province, Dawan Formation (*P. serica*; Zeng 1977, p. 37, pl. 10, figs 13–14); Sinan, Guizhou Province, Meitan Formation, Arenig (*P. serica*; M.G.B. personal observations with Rong Jia-yu); Sichuan Province, Arenig equivalent beds (*P. serica*; Xu *et al.* 1978, p. 285, pl. 115, fig. 6).

**BALTOSCANDIA:** Ingria and northern Estonia, upper Volkhovian – middle Kundan, Langevojan to Valasteian substages (*P. orbicularis*; Rubel 1961, p. 175); Öland, Sweden, Kundan, Hunderumian to lower Valasteian substages (*P. sp. A*; Jaanusson and Mutvei 1982, fig. 7).

**BRITISH ISLES:** All known occurrences are of Arenig age: Anglesey, Wales, Carmel Formation (*P. proava*; Bates 1968); Dyfed, Wales, Ogof Hen Formation and equivalents (*P. alata*; Bates 1969); Shelve inlier, Welsh Borderland, Mytton Flags (*P. cf. proava*; Williams 1974); Tourmakeady, Co. Mayo, Ireland, Tourmakeady Limestone (*P. cf. pandariana*; Williams and Curry 1985).

**FRANCE:** Montagne Noire, Couches du Foulon and lower Schistes du Landeyran (*P. cf. robusta*; Melou 1982).

#### Genus SULEVORTHIS gen. nov.

v.1948 *Sulevorthis* Jaanusson and Martna, p. 186, *nomen nudum*.

v.1982 *Sulevorthis* Jaanusson, pp. 28, 30, 33, 35, 39 (fig. 7), *nomen nudum*.

*Type species.* *Orthis lyckhohniensis* Wysogórski, 1900; from the Nabalán, Vormsian, and lower Pirguan stages (*Pleurograptus linearis* – *Dicellograptus complanatus* Zones) of Estonia.

*Derivation of name.* From Sulev, a man's name in Estonian mythology.

*Diagnosis.* Shell comparatively small, dorsal valve moderately convex, non-sulcate or only faintly sulcate, ventral interarea short, weakly apsacline. Ornament with simple costae (known range in adult specimens 13–24) and fine concentric fila. Ventral muscle field limited to delthyrial cavity, most proximal parts of ventral vascula media either adjacent over a short distance and then

divergent, or separated by a ridge and divergent from their origins. Brachiophores tabular, generally thick and elaborate with a flattened process; cardinal process a thick, simple ridge or swollen with a median crest.

*Species assigned to Sulevorthis*

*Orthis lyckholmiensis* Wysogórski, 1900 (redescribed below in order to clarify details of the type species of the genus); *Orthis playfairi* Reed, 1917; *Orthambonites bielsteini* Cooper, 1956; *Orthambonites blountensis* Cooper, 1956; *Orthambonites mostellerensis* Cooper, 1956; *Orthambonites parvicrassicostatus* Cooper, 1956; *Orthambonites rotundiformis* Cooper, 1956; *Orthambonites temesseensis* Cooper, 1956; *Orthambonites cessatus* Williams, 1963; *Orthambonites humilidorsatus* Wright, 1964; *Orthambonites exopunctatus* Williams, 1974; *Orthambonites humilidorsatus albidus* Harper, 1984; *Orthambonites humilidorsatus primadventus* Harper, 1984; *Orthambonites humilidorsatus ultimus* Harper, 1984; ?*Orthambonites rectangulatus* Cooper, 1956 (assigned with doubt as the internal features are unknown).

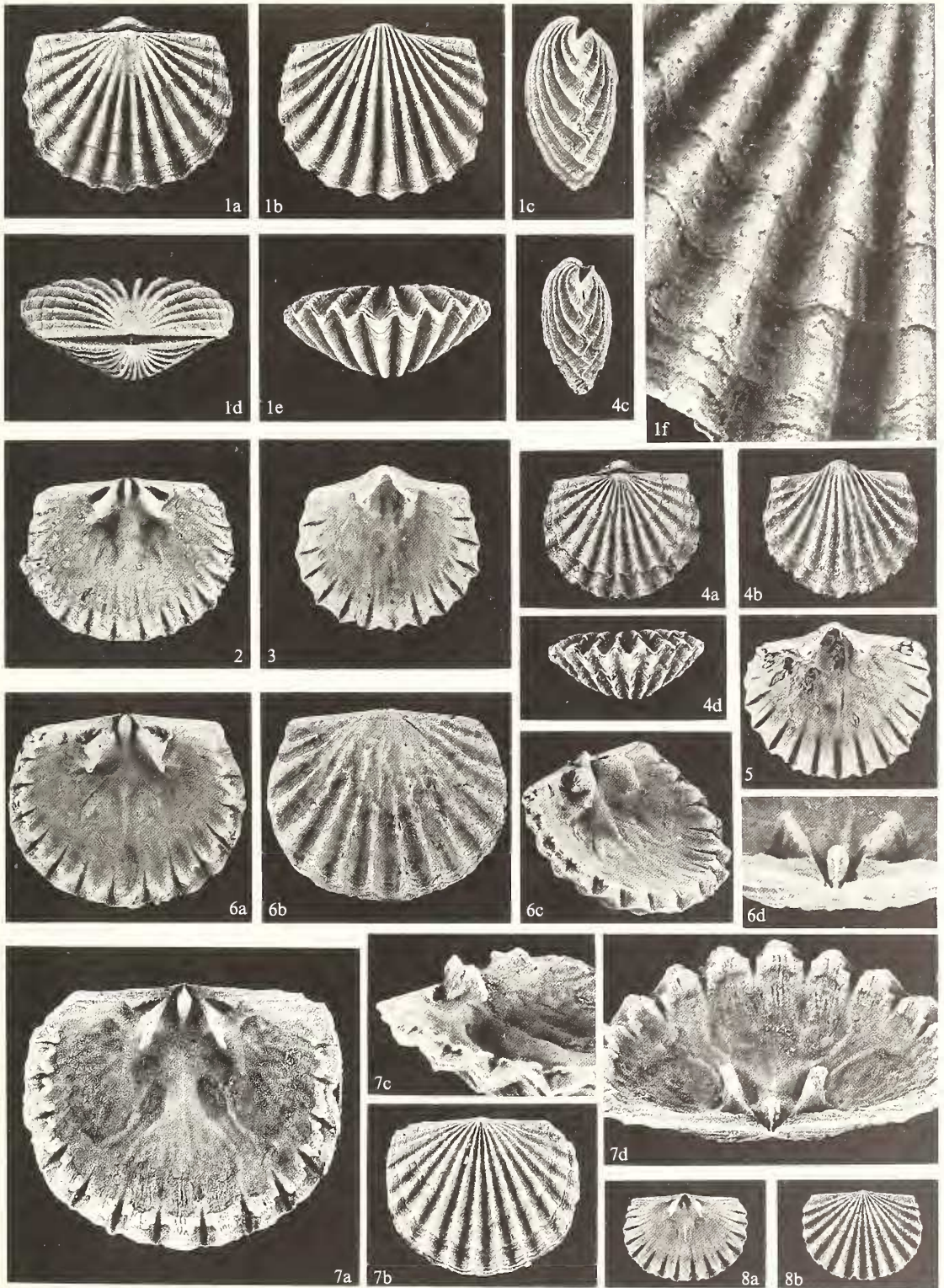
*Remarks.* This genus has long been recognized in Baltoscandia as distinct from *Orthambonites*, and this recognition has been expressed previously in use of the generic name as a *nomen nudum* (see synonymy). In all species with the external characteristics of *Sulevorthis*, the proximal ends of the ventral vascula media are either subparallel and then divergent after a short distance, or are separated by a ridge or elevation of varying width and are divergent from their origins. The former condition is shown in *S. exopunctatus* (Williams 1974, pl. 8, fig. 15) and *S. rotundiformis* (Cooper 1956, pl. 34, figs 27, 38). Williams (1974) apparently thought that this feature in *S. exopunctatus* matched the course of the vascula media in *Orthambonites*, but as noted above (p. 36), in that genus the ventral vascula media are adjacent and subparallel for most of the valve length. A ridge anterior to the ventral muscle field is developed in many species of *Sulevorthis*, and its position relative to the vascula media is shown in *S. lyckholmiensis* (Pl. 6, fig. 3a), *S. playfairi* (Williams 1962, pl. 7, fig. 41) and *S. mostellerensis* (Cooper 1956, pl. 35, figs 7, 9).

At least two described species of *Sulevorthis* show distinctive exopunctation in a pattern offset along the rib crests (*S. lyckholmiensis*, Pl. 5, fig. 1f; *S. exopunctatus* Williams 1974, pl. 8, figs 10–12). This feature may be diagnostic of the genus as a whole but has not yet been reported in other named species, possibly because of poor preservation through silicification for example; we can confirm the presence of exopunctae in numerous specimens of undescribed species from middle and upper Ordovician successions in Norway, Sweden, and Estonia. *Orthambonites* as defined in this paper has a much larger shell (the smallest true *Orthambonites* is larger than the largest known *Sulevorthis*, which has a maximum length of 12 mm) and a different micro-ornament (*Sulevorthis* lacks radial capillae). There is a conspicuous difference in the structure of the brachiophores, which in *Orthambonites* form simple, blunt bosses but which are tabular in *Sulevorthis* and in well preserved specimens have moderately long, flattened brachiophore processes that reach far beyond the socket

EXPLANATION OF PLATE 5

Figs 1–6. *Sulevorthis lyckholmiensis* (Wysogórski, 1900). All from Vormsian Stage (F<sub>1</sub>b); Kõrgessaare, Hiiumaa, Estonia. 1a–f, neotype; TAGI BR4475; dorsal, ventral, lateral, posterior and anterior views of conjoined valves, with detail of exopunctation on ribbing on left anterolateral flank of dorsal valve, a–e  $\times 3$ , f  $\times 12$ . 2, RM Br106198; interior of dorsal valve,  $\times 3$ . 3, RM Br106199; interior of ventral valve,  $\times 3$ . 4a–d, RM Br106196; dorsal, ventral, lateral and anterior views of conjoined valves,  $\times 3$ . 5, RM Br106197; interior of pedicle valve,  $\times 3$ . 6a–d, RM Br108633; interior and exterior of dorsal valve, oblique-lateral view of interior, and posterior view of cardinalia, a–c  $\times 3$ , d  $\times 5$ .

Figs 7–8. *Sulevorthis* cf. *S. lyckholmiensis* (Wysogórski, 1900). Both specimens from erratic blocks, Öland, Sweden (Hulterstad fauna, Harju Series, ?Pirguan Stage). 7a–d, RM Br4502; block 1; figured Wiman 1907, pl. 2, fig. 12–12a; interior and exterior of dorsal valve, oblique-lateral view of brachiophores, and posterior view of cardinalia, a  $\times 5$ , b  $\times 3$ , c–d  $\times 6$ . 8a–b, RM Br4501; interior and exterior of juvenile dorsal valve, block 1,  $\times 3$ .



area (Pl. 5, figs 2, 6a, c-d, 7a, c-d). It should be noted that in isolated valves of *Sulevorthis* the processes are not always preserved in their original shape, because these projections were easily worn off. However, even then the elaboration of the brachiophores is usually discernible. *Sulevorthis* is also readily distinguished from *Paralenorthis* in being non-capillate. In several regions *Sulevorthis* occurs in association with *Sivorthis* gen. nov. but it can be recognized immediately by its coarse, simple ribbing and its short ventral interarea.

*Occurrence.* *Sulevorthis* is a common genus in the Blount and Tazewell belts of the Appalachians, in the British Isles, and in Baltoscandia. Its known age range is from the mid middle to the late upper Ordovician (*Glyptograptus teretiusculus* to *Glyptograptus persculptus* Zones). In all regions it has generally previously been reported as *Orthambonites* or *Lenorthis*.

ESTONIA: Northern Estonia, Nabalán and Vormsian stages, Nybyan Substage of Pirguan Stage (*S. lyckhohmiensis*; Wysogórski 1900; Oraspöld 1959, p. 59). *Sulevorthis* is notably absent from the middle Ordovician of the North Estonian confacies belt.

SWEDEN: The genus occurs widely through the central confacies belt in the middle-upper Ordovician of Sweden, including several different undescribed species (V.J. and M.G.B. unpublished data); Öland, erratic boulders with Hultestad fauna, ?Pirguan Stage (*S. cf. lyckhohmiensis*; Wiman 1907; this paper), and lower Dalby Limestone at Böda Hamn; Östergötland, Skagen Limestone and Jonstorp Formation, and in the Hirnantian Borenshult fauna; Siljan district, Dalarna, uppermost Dalby, Skagen, Skålberg and lower Jonstorp formations, flank facies of stromatactis-bearing carbonate mounds of Kullberg Limestone (Wiman 1907, pl. 2, fig. 10) and Boda Limestone.

NORWAY: Oslo Region, Hugbergoya Shale Formation, Ashgill, Rawtheyan (*Sulevorthis* sp.; Cocks 1982, p. 758, pl. 78, fig. 5 as *Orthambonites* sp.); Hadeland, Gagnum Limestone Formation, early Ashgill (*Sulevorthis* sp. nov.; M.G.B. unpublished).

BRITISH ISLES: Shelve inlier, Welsh Borderland, Whittery Shales, Caradoc (*S. exopunctatus*; Williams 1974); Bala district, North Wales, Gelli Grin Group, Caradoc (*S. cessatus*; Williams 1963); Berwyn Hills, North Wales, Dolhir Formation, Ashgill, Rawtheyan, (*S. cf. humilidorsatus*; Hiller 1980); Girvan district, Scotland, Myoch Formation and Mill Formation of Whitehouse Group, Quarrel Hill Formation of Drummock Group, Caradoc-Ashgill, Onnian-Cautleyan (*S. humilidorsatus primadventus*, *S. humilidorsatus albidus*, *S. humilidorsatus ultimus*; Harper 1984); Girvan district, top of Stinchar Limestone to Craighead Limestone, Llandeilo-Caradoc (*S. playfairi* and *S. aff. humilidorsatus*; Reed 1917; Williams 1962); Ireland, Portrane Limestone, Ashgill, Cautleyan (*S. humilidorsatus*; Wright 1964); Ireland, Pomeroy, Killey Bridge Formation, Ashgill, Cautleyan (*S. humilidorsatus*; Mitchell 1977).

NORTH AMERICA: Southern and central Appalachians, Blount and Tazewell Belts only, *G. teretiusculus* to *D. multidentis* equivalents, inclusive: Tennessee and Virginia, Arline Formation (*S. blountensis*; Cooper, 1956); Virginia, Maryland and Pennsylvania, Martinsburg, Oranda, Benbolt and Shippensburg Formations (*S. bielsteini*; Cooper 1956); Virginia, Benbolt, Effna, Botetourt and Chatham Hill Formations (*S. parvicrassicostratus*; Cooper, 1956); Alabama, Little Oak Formation (*S. mostellerensis*; Cooper 1956); Tennessee, Athens Formation (*S. rotundiformis*; Cooper 1956); Tennessee, Alabama and Virginia, Arline, Little Oak and Botetourt Formations (*S. tennesseensis*; Cooper 1956); Maryland, Shippensburg Formation (?*S. rectangularis*; Cooper 1956).

Specimens described as '*Orthambonites parvicrassicostratus* Cooper, 1956 by Nikitin and Popov (1984, p. 134, pl. 15, figs 1-2, 4, 7-8), from the middle Ordovician of the Chingiz mountains, Kazakhstan, do not appear to belong to this species; they differ from Cooper's material in having a more strongly convex dorsal valve and, particularly, a distinctly longer ventral interarea. On the basis of the latter feature we doubt that the Kazakhstan specimens belong to *Sulevorthis*, but their true generic identity requires further study.

### *Sulevorthis lyckhohmiensis* (Wysogórski, 1900)

Plate 5, figs 1-6; Plate 6, fig. 3

- \*1900 *Orthis lyckhohmiensis* Wysogórski, p. 12, pl. 8.
- cf.v.1907 *Orthis lyckhohmiensis* Wysogórski; Wiman, p. 8, pl. 2, figs 9, 11-12a [non fig. 10 = *Sulevorthis* sp. nov.].
- cf.v.1948 *Sulevorthis* cf. *lyckhohmiensis* (Wysogórski) Jaanusson and Martna, p. 186 [generic name as *nomen nudum*].

- v.1956 'Orthis' *lyckholmiensis* Wysogórski; Jaanusson, p. 382 [name only].  
 v.1959 *Orthis(?) lyckholmiensis* Wysogórski; Oraspöld, p. 57, pl. 2, figs 1-4.  
 1964 *Orthambonites lyckholmiensis* [(Wysogórski)] Wright, p. 161 [name only].

*Neotype* (designated here). TAGI Br4475, conjoined valves.; Pl. 5, fig. 1a-f; from Kõrgessaare, island of Hiiumaa, Estonia; Kõrgessaarean Substage, lower part of Vormsian Stage (F<sub>1b</sub>), upper Ordovician (*Pleurograptus linearis* Zone); this horizon is equivalent to the low middle part of the Lyckholm Beds of former usage (Jaanusson 1944, 1956).

*Discussion.* Wysogórski's original material of *Orthis lyckholmiensis* is lost, but his brief description and illustration leave no doubt that it is the species that occurs fairly commonly in the 'Lyckholm Beds' of northern Estonia. In the absence of collections from Estonia, the species has generally been interpreted in terms of material described by Wiman (1907) under the same name from erratic blocks of upper Ordovician Hulterstad limestone (Jaanusson and Mutvei 1982) on Öland, Sweden. Our studies, however, indicate that the Öland material differs slightly from the Estonian forms (see Remarks below), and we consider it necessary to choose a neotype to clarify the definition of the species in its original sense. Apart from studying large collections in Estonia, including the material described by Oraspöld (1959), our interpretation is also based on further material housed in Stockholm (RM Br106196-Br106201, Br108633-Br108634).

*Description.* Subequally biconvex to slightly ventribiconvex, ventral valve uniformly curved, dorsal valve with very weak sulcus at the umbo, tending to die out anteriorly, maximum thickness close to 45 per cent of maximum width. Outline slightly transverse, suboval, 90 per cent as long as wide (OR 87-15-91-74; n = 4 pedicle valves), dorsal valves about 92 per cent as long as ventral valves. Cardinal angles obtusely rounded, produced as very short ears in some specimens, hinge width 85 per cent (OR 78-7-92-7; n = 6) of maximum width which is close to the mid-length. Lateral margins evenly curved or with a slight constriction immediately anterior to the hinge, anterior margin smoothly rounded. Commissures crenulate, anterior commissure rectimarginate. Ventral umbo rounded, beak suberect to weakly curved up to the hinge, dorsal umbo flattened, beak protruding slightly above lateral areas of cardinal margin. Ventral interarea short, flat to very gently concave, weakly apsacline, dorsal interarea flat, anacline. Delthyrium broad, open, apex rounded, delthyrial angle about 80°-90°, notothyrium open; both the notothyrium and base of the delthyrium are occupied by the posterior tip of the cardinal process.

Ornament costate, almost invariably with 14 or 15 costae in mature shells. Six costae in a 5 mm arc at the 5 mm growth stage of the dorsal valve. Ribs are initially low and rounded, becoming more angular but with slightly rounded crests, wavelength *c.* 1.5 mm in mature shells, amplitude *c.* 0.7-0.8 mm, interspaces weakly rounded to subflattened. Concentric ornament of fine, slightly lamellose fila and coarser growth lines. In well preserved specimens, minute but distinct exopunctae are visible just below the rib crests, normally arranged in offset pairs alongside the crests (Pl. 5, fig. 1f), but also singly in some specimens.

Delthyrial chamber broad and deep, with a small pedicle callist visible in some specimens. Teeth deltidiodont, weakly hollowed on their dorsal faces, which are bluntly triangular in outline, inner faces merging smoothly with delthyrial margins and bearing elongated, anteriorly widening fossettes. Dental plates short, receding and inclined gently inwards onto the floor of the valve. Lateral cavities shallow.

Ventral muscle field large, cordate, well impressed, widest at the base of the dental plates, unbounded outside the delthyrial chamber, occupying about 27 per cent of the valve width and up to 45 per cent of the length. Diductor scars large, tapering anterior to the dental plates, separated posteriorly by a very low flat ridge bearing the adductor scars; anterior to the adductors the elongated extensions of the diductor scars are set slightly lateral to the ridge, which in some specimens is produced into the anterior half of the valve as a low, rounded swelling. Ventral vascular system saccate, with broad, weakly divergent vascular media in shallow grooves arising at the elongate terminations of the diductor scars and branching well before the crenulations around the periphery of the valve.

Cardinalia fairly robust, set on a low notothyrial platform that is produced anteriorly either as a low, broad swelling or as a broad, rounded median ridge extending just beyond the mid-length of the valve; in some specimens the ridge tapers and extends beyond this point. Cardinal process with a simple, stout, rounded shaft merging smoothly into the median ridge, and a posteriorly directed attachment face that may protrude well above the valve margin and in some specimens is crenulated with a carinate crest.

Brachiophores robust, suberect, divergent anterolaterally at about 75° to one another, inner faces tabular, tops straight, distal edges straight to gently curved. Weakly swollen bases support the brachiophores for about

80 per cent of their length and merge smoothly into the floor of the valve to form posterolateral boundaries to the muscle field. Sockets deep, well developed, widening anterolaterally where they are bounded by rounded fulcral plates that extend as swellings onto the lateral faces of the brachiophores leaving a deep hollow in the face in its distal half. Muscle field subquadrate to subrounded, weakly quadripartite, well impressed, set in a hollow with no lateral and anterior bounding ridges, occupying about 40 per cent of the valve width and 50–55 per cent of the length. Vascular system apocopate, with well preserved intervascular ridges extending back across the muscle field.

The periphery of both valves is scored by long, strong crenulations that occupy about 25 per cent of the total length. The crenulations form broad, flat to weakly hollowed, scalloped ridges separated by narrow deep grooves.

*Dimensions of figured specimens*

	Maximum length ventral valve	Maximum length dorsal valve	Maximum width	Hinge width	Maximum thickness	Maximum number of ribs along commissure
TAGI Br4475, conjoined valves, Neotype	9.5	8.8	10.9	10.1	4.8	14
RM Br106196, conjoined valves	7.3	6.7	8.1	7.1	3.5	14
RM Br106197, ventral valve	8.3	—	9.7	—	2.7	15
RM Br106198, dorsal valve	—	8.7	10.7	8.7	1.9	15
RM Br106199, ventral valve	8.8	—	9.6	7.8	3.8	14
RM Br108633, dorsal valve	—	10.4	12.2	9.6	2.8	15
RM Br108634, ventral valve	10.0	—	10.9	9.6	3.5	15

*Occurrence.* *S. lyckholmiensis* is a common species through the Vormsian Stage of northern Estonia, and was also recorded by Jaanusson (1956) and Oraspöld (1959) from the underlying Nabalan Stage and the overlying Nybyan Substage of the Pirguan Stage.

*Remarks.* Wiman (1907, p. 8) described *lyckholmiensis* from Öland, Sweden in silicified material

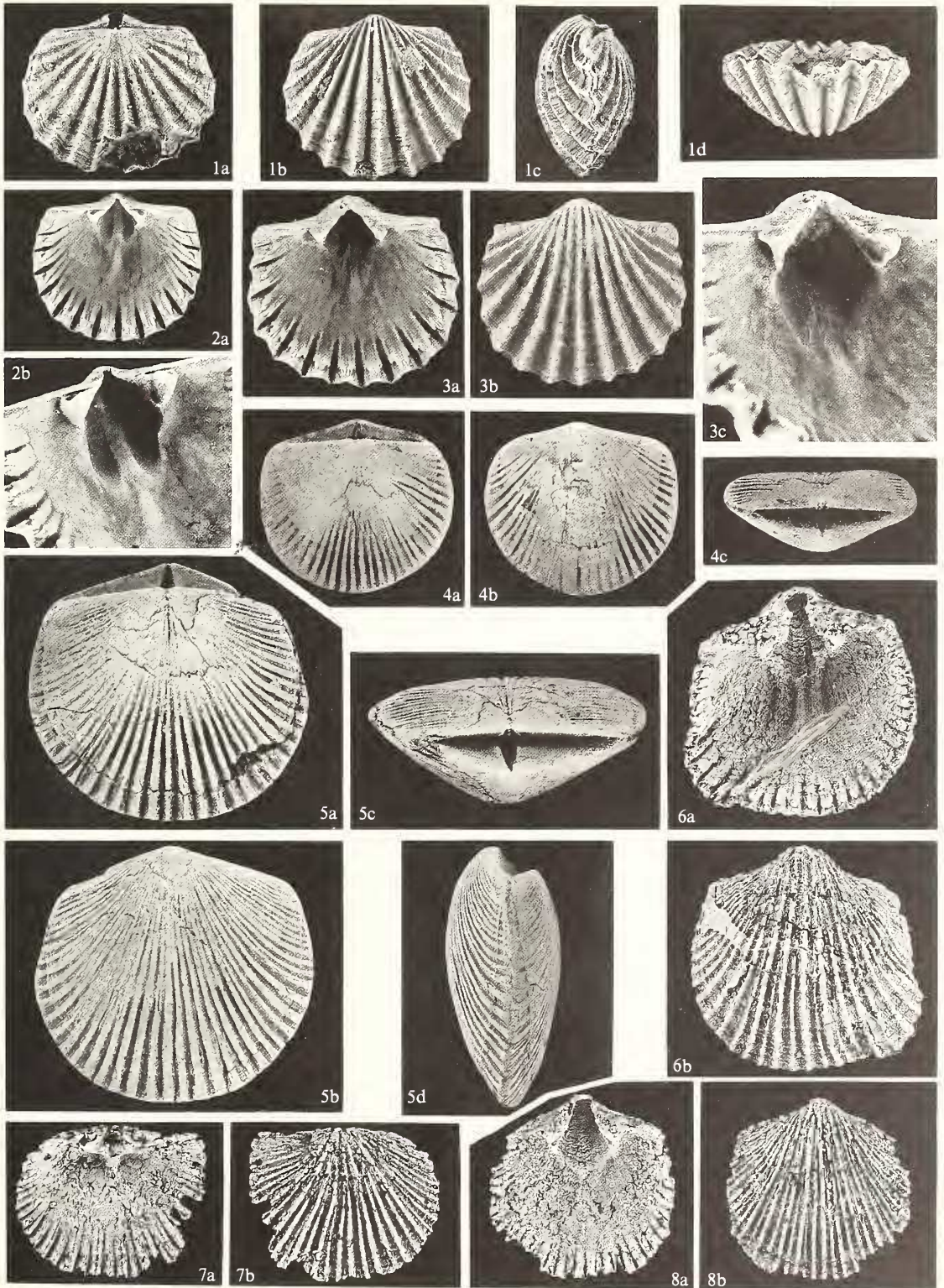
EXPLANATION OF PLATE 6

Figs 1–2. *Sulevorthis* cf. *S. lyckholmiensis* (Wysogórski, 1900). Both specimens from erratic blocks, Öland, Sweden (Hulterstad fauna, Harju Series, ?Pirguan Stage). 1a–d, RM Br4503; block 54; figured Wiman 1907, pl. 2, fig. 9; dorsal, ventral, lateral and anterior views of conjoined valves,  $\times 3$ . 2a–b, RM Br5004; block 1; figured Wiman 1907, pl. 2, fig. 11–11a; interior of ventral valve ( $\times 3$ ) with oblique view showing stout dental plates and fossettes on inner faces of teeth ( $\times 6$ ).

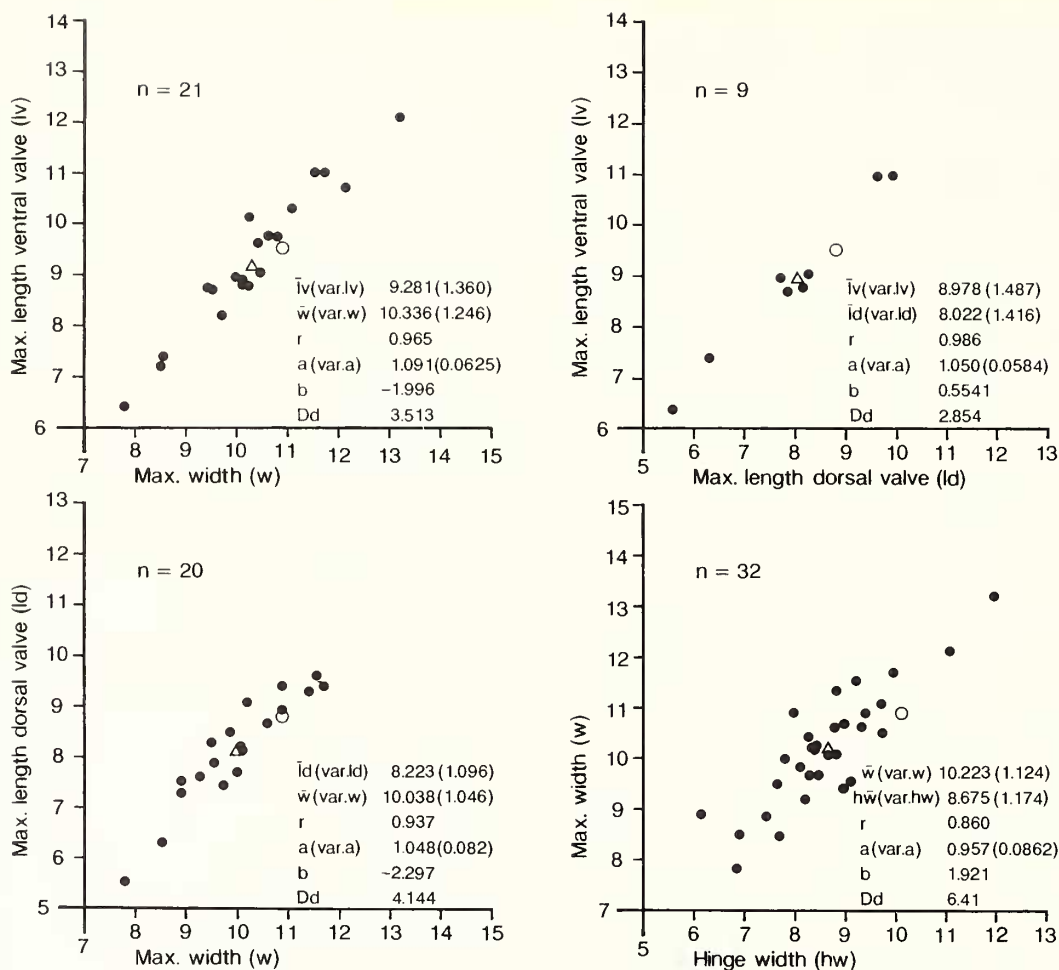
Fig. 3. *Sulevorthis lyckholmiensis* (Wysogórski, 1900). 3a–c, RM Br108634; Vormsian Stage (F<sub>1</sub>b); Kõrgessaare, Hiiumaa, Estonia; interior and exterior of ventral valve, with oblique view of delthyrial area (note the posteriorly separated vascular tracks), a–b  $\times 3$ , c  $\times 6$ .

Figs 4–5. *Shoshonorthis? ovata* Pander, 1830. 4a–c, RM Br73933; Kundan Stage; Ingria, Russia (exact horizon and locality unknown); dorsal, ventral and posterior views of conjoined valves;  $\times 2.5$ . 5a–d, neotype; RM Br116406; horizon and locality as for fig. 4; dorsal, ventral, posterior and lateral views of conjoined valves;  $\times 2.5$ .

Figs 6–8. *Sivorthis eucharis* (Ulrich and Cooper, 1938). All from upper Pogonip Group, Whiterock Series; ridge east of Frenchman Flat, Las Vegas quadrangle, Nevada, USA. 6a–b, RM Br87636; interior and exterior of ventral valve,  $\times 3$ . 7a–b, RM Br87639; interior and exterior of dorsal valve,  $\times 3$ . 8a–b, RM Br87637; interior and exterior of ventral valve,  $\times 3$ .



JAANUSSON and BASSETT, *Sulevorthis*, *Shoshonorthis*?, *Sivorthis*



TEXT-FIG. 2. Bivariate plots and statistical characterization of a topotype sample of 32 specimens of *Sulevorthis lyckholmiensis* (9 conjoined valves, 12 ventral valves, 11 dorsal valves); same sample as used for Table 1. The open circle represents the plot of the neotype in each graph, with other specimen values plotted as solid circles; the triangle is a plot of the mean value for the sample.

etched from erratic blocks containing the Hultestad fauna; the precise age of this material is uncertain, but it is possibly from Pirguan equivalents in Estonia (Ashgill, *Dicellograptus complanatus* and *D. anceps* Zones; Jaanusson and Mutvei 1982, p. 9) and thus slightly younger than the type material of *S. lyckholmiensis*. The small sample and silicified preservation of the Öland specimens makes comparison uncertain, but there is some suggestion that they are slightly more globose, with more elaborate brachiophore processes and a more anteriorly lobate ventral muscle field than the Estonian material; these relatively small differences may be of only intraspecific significance, but until the uncertainties and age relationships are resolved we identify the Öland specimens as *S. cf. lyckholmiensis* (Pl. 5, figs 7–8; Pl. 6, figs 1–2). Wright (1964, p. 163) similarly drew attention to differences between *lyckholmiensis s.s.* and the Swedish material described by Wiman (1907), and he considered that the latter might be related more closely to or even conspecific with *S. humilidorsatus* (Wright) from the Portrane Limestone (Ashgill) of Ireland. Some of the differences described by Wright are somewhat variable in the full range of material available from Öland, over and above that figured by Wiman, and in the light of the uncertainties mentioned above we consider an



TABLE 1. Statistics from a sample of 32 topotype specimens of *Sulevorthis lyckholmiensis*; Vormsian, Kõrgessaare, Hiiumaa, Estonia; sample housed in the Geological Institute, Estonian Academy of Sciences, Tallinn; lv = maximum length ventral valve, ld = maximum length dorsal valve, w = maximum width, hw = hinge width, t = thickness (conjoined or single valves as appropriate).

A CONJOINED VALVES; n = 9					
Variates	lv	ld	w	hw	t
Means	8.99	8.04	10.10	8.73	4.72
Variance-covariance matrix	2.21	2.07	1.90	1.46	1.22
		2.00	1.81	1.52	1.12
			1.68	1.37	1.02
				1.50	0.72
					0.72

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B VENTRAL VALVES; n = 12				
Variates	lv	w	hw	t
Means	9.52	10.60	9.18	3.52
Variance-covariance matrix	1.62	1.48	1.36	0.61
		1.50	1.42	0.50
			1.53	0.50
				0.30

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C DORSAL VALVES; n = 11				
Variates	ld	w	hw	t
Means	8.41	10.0	8.15	1.90
Variance-covariance matrix	0.59	0.59	0.44	0.37
		0.72	0.53	0.32
			0.70	0.36
				0.39

identification as *S. cf. lyckholmiensis* to be more appropriate. Wright's text (1964, p. 163) implies that all of Wiman's (1907) material is from Dalarna in Sweden; in fact, of the figured specimens, only Wiman's pl. 2, fig. 10 is from Dalarna (Kullberg Limestone, late Caradoc), with the remainder from the Hulterstad fauna of Öland. We consider that the Kullberg Limestone *Sulevorthis* belongs to a new species (see p. 40 and synonymy, p. 40). Reed (1932, pp. 116, 117, 132, pl. 20, fig. 18) described a species as *cf. lyckholmiensis* from the upper Ordovician of the Trondheim region, Norway, but his reported presence of 'fine radial striae' on the ornament (i.e. capillae) suggests that this material does not belong to *Sulevorthis*.

#### Genus SIVORTHIS gen. nov.

*Type species. Sivorthis filistera* sp. nov.; from the lower Dalby Limestone (near base of *Nemagraptus gracilis* Zone), Böda Hamn, Öland, Sweden.

*Derivation of name.* From Siv, the wife of Thor in Scandinavian mythology.

*Diagnosis.* Shell small to medium sized, dorsal valve moderately convex, non-sulcate to weakly sulcate, ventral interarea relatively long, fairly strongly apsacline. Costellate (known range of ribs 27–46 in adult valves), one or two generations of costellae intercalated in front of the umbo. Ventral muscle field relatively small, anterior margin almost straight to slightly rounded. Ventral vascula media parallel for about half of their extent between the muscle field and anterior valve margin, then

broadly curved laterally (in at least two species). Brachiophores with relatively slender bases and a laterally compressed process; cardinal process a simple ridge, mostly slender.

*Species assigned to Sivorthis*

*Sivorthis filistera* sp. nov. (see description below); ?*Orthis* (*Plectorthis*) *ardmillanensis* Reed, 1917; *Orthis eucharis* Ulrich and Cooper, 1938; *Orthambonites bellus* Cooper, 1956; *Orthambonites friendsvillensis* Cooper, 1956; *Orthambonites multicostellatus* Cooper, 1956; *Orthambonites occidentalis* Cooper, 1956; *Orthambonites tenuicostatus* Cooper, 1956; ?*Orthambonites minus* Cooper, 1956; ?*Orthambonites minutus* Cooper, 1956.

*Discussion.* With a maximum recorded shell length of 15 mm, *Sivorthis* is typically much smaller than known species of *Orthambonites*, from which it is also readily distinguished externally by its considerably longer and more strongly apsacline ventral interarea and by the consistent development of costellae. The stout, simple brachiophores and long, subparallel ventral vascula media of *Orthambonites* contrast with the more compressed to tabular brachiophores and divergent vascular tracks of *Sivorthis*. Similar differences in ornamentation and in the cardinalia also separate *Sivorthis* from *Paralenorthis*. From *Sulevorthis*, which has adult shells of about the same maximum size, *Sivorthis* differs in having a relatively longer and more strongly apsacline ventral interarea, finely costellate ribbing, and more delicately constructed brachiophore bases; in *Sulevorthis* the tabular brachiophores are invariably supported by massive bases with thick secondary shell developed. The costellate ribbing of *S.?* *arduillaueensis* (Reed, 1917; Williams 1962, pl. 8, fig. 8) is of *Sivorthis* type, but this small species is otherwise poorly known.

The parallel course of the proximal portions of the ventral vascula media is indicated in specimens of *S. bella* (Cooper, 1956, pl. 35, fig. 48) and *S. friendsvillensis* (Cooper, 1956, pl. 36, fig. 8), and can be observed clearly in *S. eucharis* (Pl. 6, fig. 6a) and *S. filistera* (Pl. 7, figs 3a, 6b), in which the laterally curved continuation of the medial vascular tracks is also preserved in some ventral interiors.

Most of the known specimens of species assigned above to *Sivorthis* are silicified and the micro-ornament is obliterated or very poorly preserved. However, *S. tenuicostatus* has well defined concentrically lamellose fila (Pl. 7, figs 8b, 9), and examination of specimens of *S. bella* in the United States National Museum has revealed traces of similar sculpture. In other North American species no undoubted trace of the micro-ornament could be observed to compare with the fila and capillate pattern of *S. filistera*.

The distal part of the brachiophores is preserved only exceptionally in silicified specimens of *Sivorthis*. A specimen of *S. bella* shows somewhat compressed brachiophore processes (Cooper 1956, pl. 35, fig. 49 and personal observations), and the presence of a similar brachiophore structure is indicated in *S. friendsvillensis* (Cooper 1956, pl. 36, fig. 1). The general tabular shape of the processes resembles that of *Sulevorthis*.

*Occurrence.* With the exception of occurring also in the Great Basin of the western USA and in Oklahoma, known species of *Sivorthis* appear to have roughly the same geographical distribution as *Sulevorthis*. However, *Sivorthis* appears earlier, in rocks of Whiterock (Llanvirn equivalent) age and is not known to continue into the upper Ordovician. Occurrences in the southern Appalachians are restricted to the Blount confacies belt.

SWEDEN: Öland (central Baltoscandian confacies belt), lower Dalby Limestone, Viruan (*S. filistera* sp. nov.; see below).

BRITISH ISLES: Girvan district, Scotland, basal Ardwell Mudstones, Caradoc, lower *Diplograptus multidentis* Zone (*S.?* *ardmillanensis*; Reed 1917; Williams 1962).

NORTH AMERICA: Whiterock Series: Nevada, Antelope Valley Limestone (*S. occidentalis*; Cooper 1956) and upper Pogonip Group (*S. eucharis*; Ulrich and Cooper 1938); Utah, upper part of Garden City Formation (*S. cf. eucharis*; Ross 1968, p. H6, pl. 3, figs 1-7); Oklahoma, *G. teretiusculus* Zone equivalents, Tulip Creek Formation (*S.?* *minus*; Cooper 1956) and McLish Formation (*S.?* *minutus*; Cooper 1956). Southern Appalachian occurrences are all in *G. teretiusculus* to *D. multidentis* Zone equivalents: Virginia, Chatham Hill Formation (*S. bella*; Cooper 1956), and Edinburg and Oranda Formations (*S. multicostellata*; Cooper 1956);

Tennessee, Arline Formation (*S. friendsvillensis*; Cooper 1956); Alabama, Pratt Ferry Formation (*S. tenuicostata*; Cooper 1956).

*Sivorthis filistera* sp. nov.

Plate 7, figs 1–7

*Derivation of name.* Latin 'filum', a thread – provided with threads; referring to the fine capillae and well developed, lamellose growth fila.

*Holotype.* RM Br116395, conjoined valves, lower Dalby Limestone (Viruan, approximately at base of *Nemagraptus gracilis* Zone), Böda Hamn, north-east Öland, Sweden; Pl. 7, fig. 1a–e.

*Paratypes.* RM Br116371–Br116394, Br116396–Br116405, Br17368, Br18287, Br16013–Br16015, all from same locality and horizon as holotype. RM Br18086–Br18087, from loose blocks of lower Dalby Limestone at Bocketorp, Oland, Sweden.

*Diagnosis.* Finely costellate (40–46 ribs observed) with well developed lamellose growth fila. Ventral interarea relatively long. Sockets confined within notothyrial platform, fulcral plates absent, dorsal median ridge tapering almost to anterior margin.

*Description.* Ventribiconvex, ventral valve uniformly curved transversely and longitudinally, dorsal valve only weakly to moderately convex with slightly swollen umbo and faint sulcus occupying median half of valve behind the umbo; maximum thickness approximately 45 per cent of maximum width. Outline subtriangular in some juvenile shells, becoming subrounded to subquadrate at maturity, subequally as long as wide (OR 82.96–104.61 per cent in 14 ventral valves), lateral margins almost straight to weakly curved, anterior margin smoothly curved; dorsal valves 83–91 per cent as long as ventral valves ( $n = 8$  conjoined specimens). Cardinal angles gently rounded, hinge width equals maximum width in young shells, but at maturity the point of maximum width is close to mid length and hinge width is then approximately 90 per cent of maximum width (OR 82.3–100;  $n = 12$ ). Commissures crenulate, anterior commissure weakly sulcate. Ventral umbo rounded, beak erect, dorsal umbo obscure to slightly swollen; ventral interarea relatively long, apsacline, plane to weakly concave, from about three to six times as long as the plane, anacline dorsal interarea. Delthyrium and notothyrium open, delthyrium narrow with rounded apex, delthyrial angle generally less than  $45^\circ$ , margins approaching subparallel in some specimens; cardinal process extends up into notothyrium.

Ornament costellate, most commonly with only one generation of branching. Ribs are low and rounded, equally spaced with an amplitude of about 0.7 mm at the commissure of mature shells, and number 14 to 16 in a 5 mm arc at the 5 mm growth stage of the dorsal valve. Interspaces subrounded. Fine capillae present on costellae and in interspaces, with a maximum of three observed between ribs, of which the central capilla then tends to be slightly stronger; fine but distinctly lamellose growth fila are preserved over and between the costellae (often worn away in the available samples).

Delthyrial chamber relatively broad and deep. Teeth blunt, deltidiodont with triangular dorsal faces which may be weakly concave; inner faces merge smoothly with delthyrial margins which bear elongated anteriorly widening fossettes. Dental plates short and blunt, erect, receding, lateral cavities shallow.

Ventral muscle field well impressed, subcordate, widest at the base of the dental plates from where low,

TABLE 2. Statistics from 20 syntype specimens (all conjoined valves) of *Sivorthis filistera*; lower Dalby Limestone (Viru), Böda Hamn, Öland, Sweden; sample housed at Naturhistoriska Riksmuseet, Stockholm; lv = maximum length ventral valve, ld = maximum length dorsal valve, w = maximum width, hw = hinge width, t = thickness.

Variates	lv	ld	w	hw	t
Means	11.10	9.93	12.0	10.4	5.11
Variance-covariance matrix	3.09	2.63	2.58	1.55	1.09
		2.42	2.42	1.40	0.96
			2.91	1.59	0.84
				1.27	0.52
					0.81

curved, rounded bounding ridges converge toward the anterior margin of the scars; the ridges die out anteriorly and the anteromedial part of the muscle field is either unbounded or rimmed by a very low flat pad of shell, with the anterior ends of the diductor scars separated by a shallow, broad hollow. The muscle field is slightly longer than wide, occupying about 25 per cent of the valve width and some 33 per cent of the length. Diductor scars large, longitudinally oval, widening anteriorly, separated by and extending beyond slender parallel adductor scars which are unbounded anteriorly. Ventral vascular system poorly preserved in available material, saccate with large gonadal areas bounded by weak vascula media which appear to be subparallel immediately anterior to the muscle field but curve anterolaterally at about the mid length of the valve.

Cardinalia raised on a wide platform, notothyrial cavity long, occupied by a slender, simple cardinal process which may be only slightly swollen anteriorly; the process merges smoothly into the anterior edge of the notothyrial platform which is produced anteriorly as a broad, rounded median ridge. Brachiophores poorly preserved in available material, but apparently simple and tabular. Sockets small, slightly elongated and relatively deep, excavated entirely within the lateral area of the notothyrial platform. No fulcral plates. Dorsal muscle field relatively large, subquadrate, occupying up to 30 per cent of valve width, unbounded laterally and anteriorly. Posterior adductor scars set immediately under anterior end of notothyrial platform, suboval, larger and deeper than the weakly impressed anterior scars. The broad, low, rounded median ridge occupies almost 50 per cent of the width of the muscle field, becoming lower between the anterior scars where it tapers to a narrow pad that extends almost to the anterior margin of the valve. Mantle canal system only weakly impressed but apparently digitate, with long vascula media extending from anterior muscle scars almost to anterior margin and only weakly divergent from median ridge, and large vascula genitalia occupying most of the posterolateral quarters of the valve.

The periphery of both valves is crenulated by strong, flat ridges separated by narrower, rounded grooves.

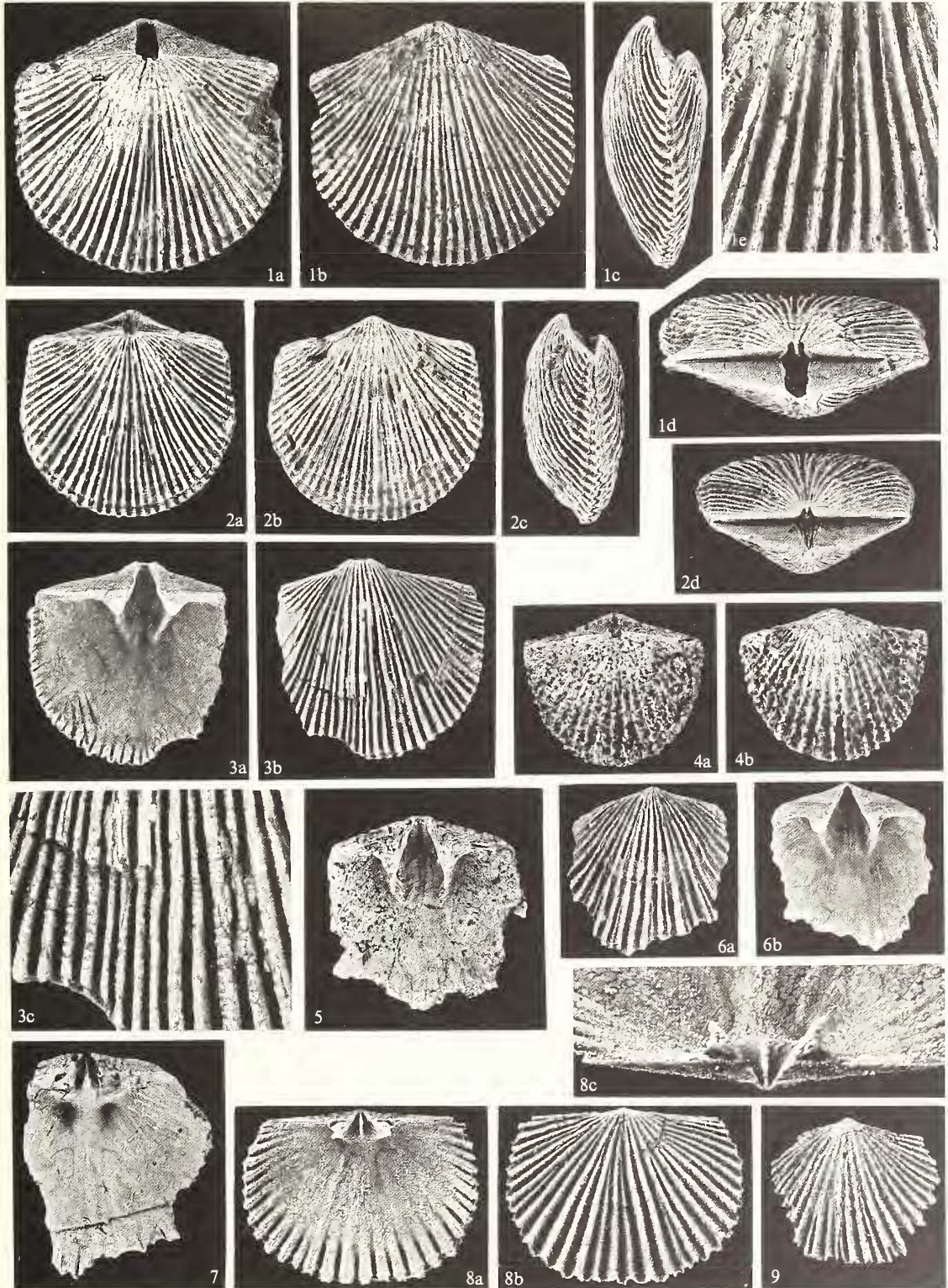
#### *Dimensions of figured specimens*

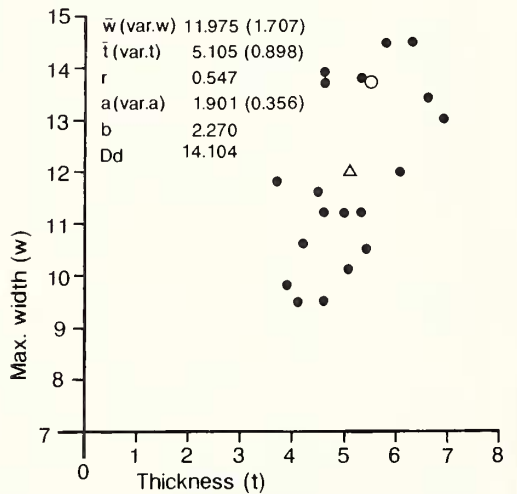
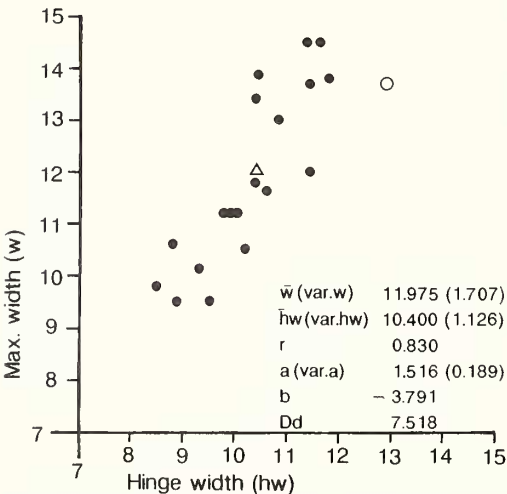
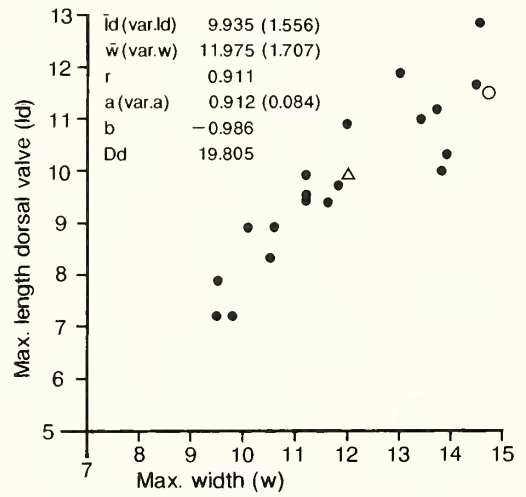
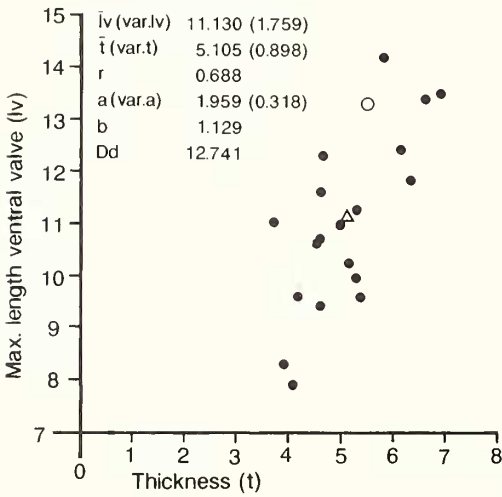
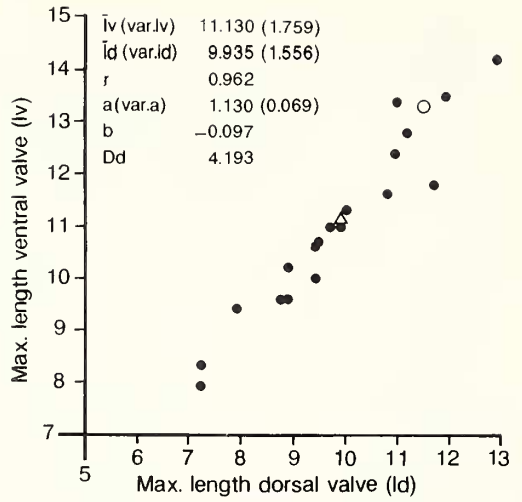
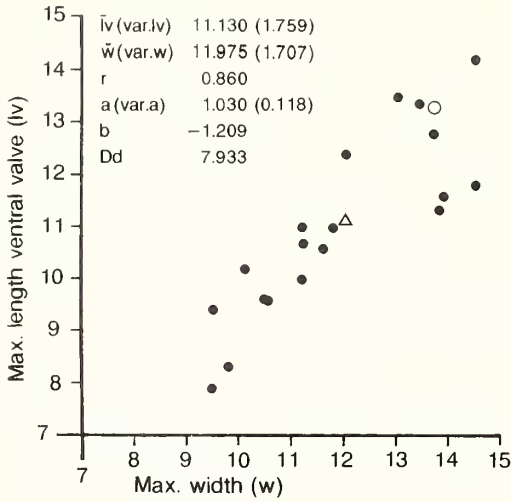
	Maximum length ventral valve	Maximum length dorsal valve	Maximum width	Hinge width	Maximum thickness	Maximum number of ribs along commissure
RM Br116395, conjoined valves, Holotype	13.3	11.5	13.7	12.9	5.5	44
RM Br116397, conjoined valves, Paratype	11.0	9.9	11.2	10.0	5.0	46
RM Br116390, ventral valve, Paratype	—	—	—	—	2.3	—
RM Br116391, ventral valve, Paratype	10.5	—	—	—	3.1	—
RM Br116392, ventral valve, Paratype	—	—	—	—	2.6	—
RM Br116393, dorsal valve, Paratype	—	—	—	—	1.3	—
RM Br116371, conjoined valves, Paratype	7.9	7.2	9.5	9.5	4.1	—

#### EXPLANATION OF PLATE 7

Figs 1-7. *Sivorthis filistera* sp. nov. All from lower Dalby Limestone, Viru Series; Böda Hamn, north-east Öland, Sweden. 1a-c, holotype; RM Br116395; dorsal, ventral, lateral and posterior views of conjoined valves, with detail of branching costellae, a-d × 3, e × 8. 2a-d, paratype; RM Br116397; dorsal, ventral, lateral and posterior views of conjoined valves, × 3. 3a-c, paratype; RM Br116391; interior and exterior of ventral valve, with detail of lamellose micro-ornament, a-b × 3, c × 8. 4a-b, paratype; RM Br116371; dorsal and ventral views of juvenile conjoined valves, × 3. 5, paratype; RM Br116390; interior of ventral valve, × 3. 6a-b, paratype; RM Br116392; exterior and interior of ventral valve, × 3. 7, paratype; RM Br116393; interior of dorsal valve, × 3.

Figs 8-9. *Sivorthis tenuicostata* (Cooper, 1956). Both from Pratt Ferry Formation; Pratt Ferry, Alabama, U.S.A. 8a-c, RM Br135164; interior and exterior of dorsal valve (× 3), with posterior view of cardinalia (× 6). 9, RM Br135165; exterior of ventral valve, × 3.





TEXT-FIG. 3. Bivariate plots and statistical characterization of a sample of 20 syntype conjoined valves of *Sivorthis filistera*; same sample as used for Table 2. Symbols as for Text-fig. 2 (but with open circle here as holotype).

*Remarks.* *S. filistera* is distinct from other species referred to *Sivorthis* in having finer ribbing. It appears to be closest to *S. tenuicostata* (Cooper), in which 34–40 costellae are typically developed, and which has a slightly more convex ventral valve and a posteriorly more convex dorsal valve. Other species are distinguished readily by still coarser ribbing.

*Occurrence.* *S. filistera* is currently known only from the lower Dalby Limestone on Öland, Sweden.

#### Genus SHOSHONORTHIS gen. nov.

*Type species.* *Orthis michaelis* Clark, 1935; from the Swan Peak Formation (Whiterock) of Utah, USA.

*Derivation of name.* From Shoshone, a North American Indian group.

*Diagnosis.* Shell medium sized to fairly large, strongly ventribiconvex, non-sulcate to weakly sulcate, ventral interarea fairly long and apsacline. Ornament costate (known range 18–36 rounded ribs in adult valves), fine radial capillae developed in most species. Ventral muscle field long, extending considerably beyond the delthyrial cavity. Cardinalia relatively long, brachiophores developed as slender rods. Cardinal process a slender ridge without a clearly differentiated myophore. Dorsal musculature with posterior pair of scars considerably larger than the anterior pair.

#### *Species assigned to Shoshonorthis*

*Orthis michaelis* Clark, 1935; *Orthambonites swanensis* Ulrich and Cooper, 1938; *Orthambonites subconvexus* Cooper, 1956; *Orthambonites dinorthoides* Cooper, 1956; *Orthambonites perplexus* Ross, 1967; *Orthambonites tiftletensis* Havlíček, 1971; ?*Gonambonites ovata* Pander, 1830.

*Discussion.* *Shoshonorthis* is typically a medium sized to fairly large shell (recorded maximum length up to 21 mm). Its relatively long ventral interarea distinguishes it immediately from *Orthambonites*, and internally the former genus is also recognized easily by its considerably longer ventral muscle field and relatively longer cardinalia; similarities in other general external features are probably due to parallel development. Distinction between *Shoshonorthis* and early species of *Plectorthis* is less clear, partly because the internal characters of the latter are poorly known. The dorsal valve of *Shoshonorthis* is normally less convex than in *Plectorthis*, and the brachiophore supports are not developed as discrete plates. *Plectorthis* also lacks the capillate micro-ornament present in most species assigned here to *Shoshonorthis*.

*S. michaelis*, *S. swanensis*, *S. dinorthoides*, *S. tiftletensis* and *S. ovata* have well developed radial capillae. In *S. perplexa* there is a single capilla in each interspace between the costae (Ross 1970, p. 57); capillate micro-ornament has not been reported in *S. subconvexa*.

Cooper (1956, p. 301) emphasized the similarity in the shape of the ventral muscle field between *S. dinorthoides* and species of *Dinorthis*, obviously based on a ventral interior that he figured (1956, pl. 33, fig. 27). However, in another figured ventral interior (1956, pl. 33, fig. 26) the configuration of the muscle field is very similar to that of *S. subconvexa* (see Cooper 1956, pl. 34, fig. 26), indicating some variation in this feature. One specimen of *S. subconvexa* shows faint traces of the ventral vascula media (Cooper 1956, pl. 34, fig. 35), which diverge anterolaterally directly from the muscle field. In other species of *Shoshonorthis* the course of the ventral vascula media is unknown.

The configuration of the dorsal muscle field is known in *S. michaelis* (Ulrich and Cooper 1938, pl. 14, fig. 26) and *S. subconvexa* (Cooper 1956, pl. 34, fig. 22); in both cases the posterior pair of scars is considerably larger than the anterior pair. In *S. tiftletensis* the structure of the cardinalia is poorly known and the assignment of this species to *Shoshonorthis* must therefore remain somewhat uncertain.

Two specimens from Pulkova (RM Br116406, Br73933) agree clearly with Pander's (1830) brief description and illustration of *Gonambonites ovata*. Pander probably included this species in *Gonambonites* because of its relatively long ventral interarea; there are no other species that he described with which this distinctive form could be confused. Although somewhat worn, the external character of both specimens conforms with the morphology of *Shoshonorthis*, but until internal features are known the generic assignment is only tentative.

*Occurrence.* All described species that we assign to *Shoshonorthis* appear to be confined to rocks of Whiterock-Llanvirn age. The genus is known currently from the Great Basin of the western USA, Oklahoma, from Ingria, and from North Africa. In addition to these occurrences of described taxa, one of us (M.G.B.) has examined specimens resembling *S. michaelis* in undescribed faunas from the early-mid Arenig age Meitan Formation of Sinan County, Guizhou Province, south-west China; this material, which occurs in association with *Paralenorthis serica*, may belong to *Shoshonorthis*, and is currently being described by Dr Rong Jia-yu (Nanjing) and his colleagues.

**NORTH AMERICA:** All occurrences are of Whiterock age: Utah, Swan Peak Formation (*S. michaelis*; Clark 1935; Ulrich and Cooper 1938, p. 101, pl. 14, figs 11–12, 21, 23, 25–29; Ross 1967, p. D3, pl. 1, figs 1–2; *S. swanensis*; Ulrich and Cooper 1938; Ross 1967, pl. 1, fig. 8); Utah, Kanosh Shale (*S. michaelis*; Jensen 1967, p. 90, pl. 4, figs 1–5); Nevada, Antelope Valley Limestone (*S. perplexa*; Ross 1967); Utah, Crystal Peak Dolomite (*S. perplexa*; Jensen 1962, p. 91, pl. 4, figs 6–10); Oklahoma, Oil Creek Formation (*S. dinorthoides*; Cooper 1956; and *S. subconvexus*; Cooper 1956).

**INGRIA:** Kundan, exact locality and horizon unknown (*S?* *ovata* (Pander, 1830) herein).

**MOROCCO:** Un-named Llanvirn or Llandeilo beds (*S. tiftletensis*; Havlíček 1971).

### GENUS ORTHIS Dalman, 1828

*Type species.* *Orthis callactis* Dalman, 1828; from the zone of *Asaphus* (*Asaphus*) *expansus* ('Expansus Limestone'; high lower Ordovician, Kundan Stage, Hunderumian Substage, high *Didymograptus hirundo* to lowest *Didymograptus bifidus* Zone), Husbyfjöl, Östergötland, Sweden.

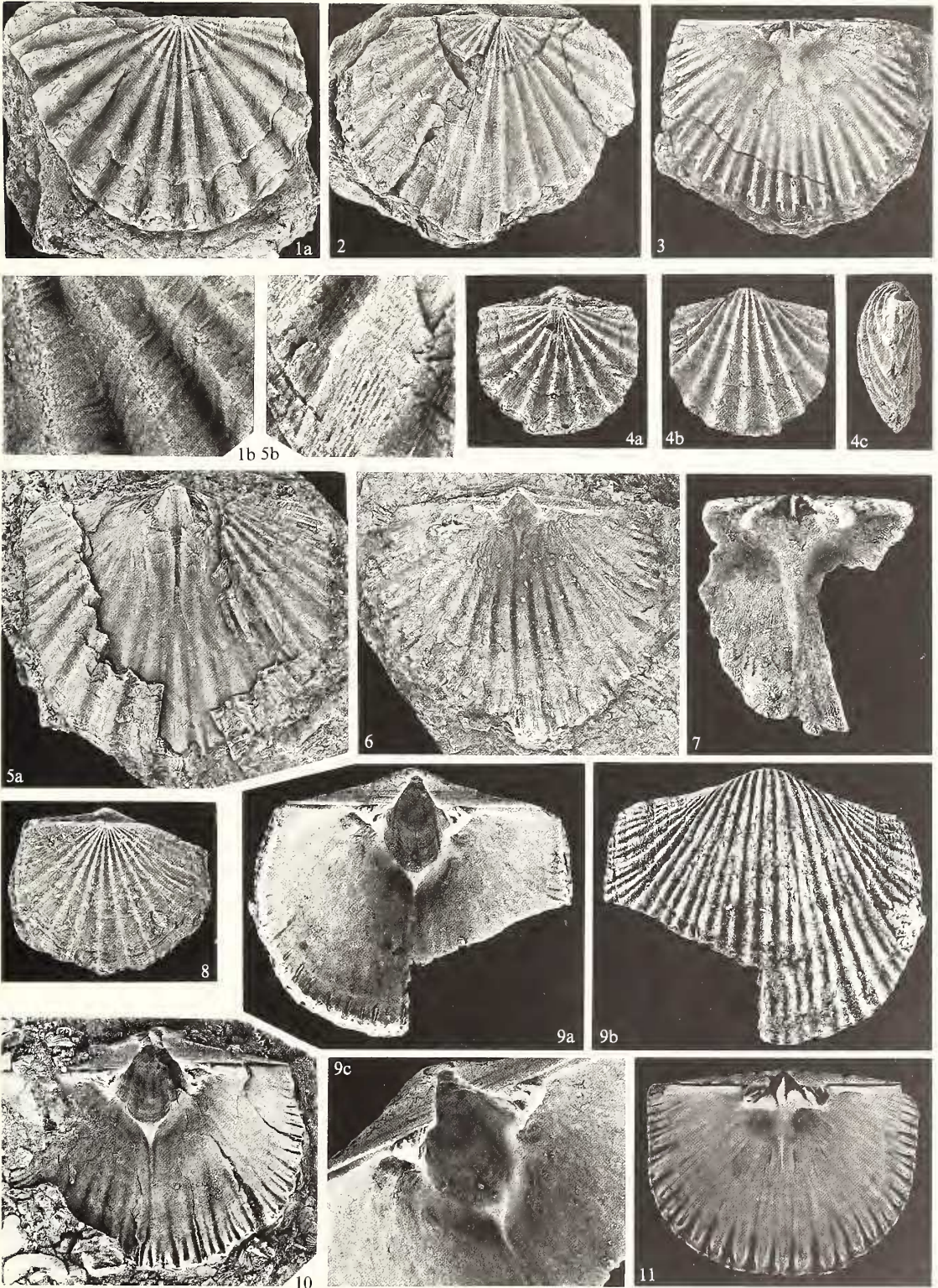
*Diagnosis.* Plano-convex to weakly concavo-convex, anterior commissure rectimarginate, shells relatively large at maturity. Ornament costate and finely capillate. Interareas short, ventral beak low. Cardinalia very short and low, notothyrial platform aligned subparallel to the hinge, brachiophores widely divergent, cardinal process a simple ridge. Dental plates short, receding, ventral muscle field extended only slightly beyond the broad, shallow, delthyrial cavity, no ventral median ridge. Ventral vascula media adjacent and parallel for about half the length of the valve.

#### EXPLANATION OF PLATE 8

Figs 1–8. *Orthis callactis* Dalman, 1828. All specimens are from the 'Expansus Limestone', lower Kundan Stage, Hunderumian Substage. 1*a–b*, lectotype; RM Br21959; figured Dalman 1828, pl. 2, fig. 2 and Hisinger 1837, pl. 20, fig. 9; Husbyfjöl, Östergötland, Sweden; exterior of dorsal valve ( $\times 2.5$ ) and detail of fine fila ( $\times 10$ ) on posterolateral flank. 2, paralectotype; RM Br21958; locality as for fig. 1; exterior of dorsal valve,  $\times 2$ . 3, RM Br22129; Omberg, Östergötland, Sweden; interior of dorsal valve,  $\times 2$ . 4*a–c*, RM Br135876; Borghamn, Östergötland, Sweden; dorsal, ventral and lateral views of juvenile conjoined valves;  $\times 2$ . 5*a–b*, RM Br134536; Locality unknown, Siljan district, Dalarna, Sweden; partly exfoliated ventral valve ( $\times 1.5$ ) and detail of finely capillate ornament on left posterolateral flank ( $\times 10$ ). 6, RM Br135165; locality as for fig. 1; interior of ventral valve,  $\times 1.5$ . 7, RM Br135166; locality as for fig. 4; interior of fragment of dorsal valve,  $\times 4$ . 8, RM Br21971; locality as for fig. 3; dorsal view of conjoined valves,  $\times 1$ .

Figs 9–11. *Glossorthis taceus* Opik, 1930. All from Kukruse Stage ( $C_{11}\alpha$ ); Kohtla-Järve, Estonia. 9*a–c*, RM Br135877; interior and exterior of ventral valve ( $\times 2$ ), with oblique view of interior ( $\times 3$ ) to show elevation of muscle platform, stout dental plates and fossettes on inner faces of teeth. 10, RM Br92206; interior of ventral valve,  $\times 2$ . 11, RM Br108635; interior of dorsal valve, distal portion of brachiophores not preserved,  $\times 2$ .





JAANUSSON and BASSETT, *Orthis*, *Glossorthis*

*Species assigned to Orthis*

Although the name *Orthis* has been assigned in the past to an extremely wide range of species, we have not identified any that we consider with certainty to be congeneric with *O. callactis*.

*Remarks.* Dalman's (1828) syntypes of *Orthis callactis* are housed in the Riksmuseum in Stockholm, which allows us to select a lectotype in order to stabilize the identity of the species and hence the type genus for the family Orthidae. Although *O. callactis* has always been interpreted fairly consistently, Dalman's material has not been illustrated or revised subsequent to its original description.

The genus *Orthis* has long been defined in an extremely wide sense, to include not only *O. callactis* but also species of *Orthambonites* and related genera. *Orthis* is readily distinguished from all other taxa described in this paper by having a plane to weakly concave dorsal valve, a very short dorsal interarea, and very short cardinalia with widely divergent brachiophores and the notothyrial platform aligned subparallel to the hinge.

*Orthis callactis* Dalman, 1828

Plate 8, figs 1–8

- v\*1828 *Orthis callactis* Dalman, p. 112, pl. 2, fig. 2.
- 1830 *Orthis crassicosta* Pander, p. 82, pl. 21, fig. 1.
- 1830 *Orthis eminentis* Pander, p. 82, pl. 21, fig. 2.
- v.1837 *Orthis callactis* Dalman; Hisinger, p. 70, pl. 20, fig. 9.
- v.1880 *Orthis callactis* Dalman var.; Lindström in Angelin and Lindström, p. 26, figs 2–3.
- 1932 *Orthis callactis* Dalman; Schuchert and Cooper, p. 75, pl. 2, figs 8, 12, 15, 17.
- v.1953 *Orthis callactis* Dalman; Alikhova, p. 28, pl. 1, figs 13–16.
- v.1961 *Orthis callactis*(?) Dalman; Rubel, p. 172, pl. 14, figs 16–17.
- 1965 *Orthis callactis* Dalman; Williams in Williams *et al.*, p. H311, fig. 197.7a–d.
- v.1985 *Orthis calligramma* Dalman; Cocks, p. 56, pl. 5.2.2.A–B.

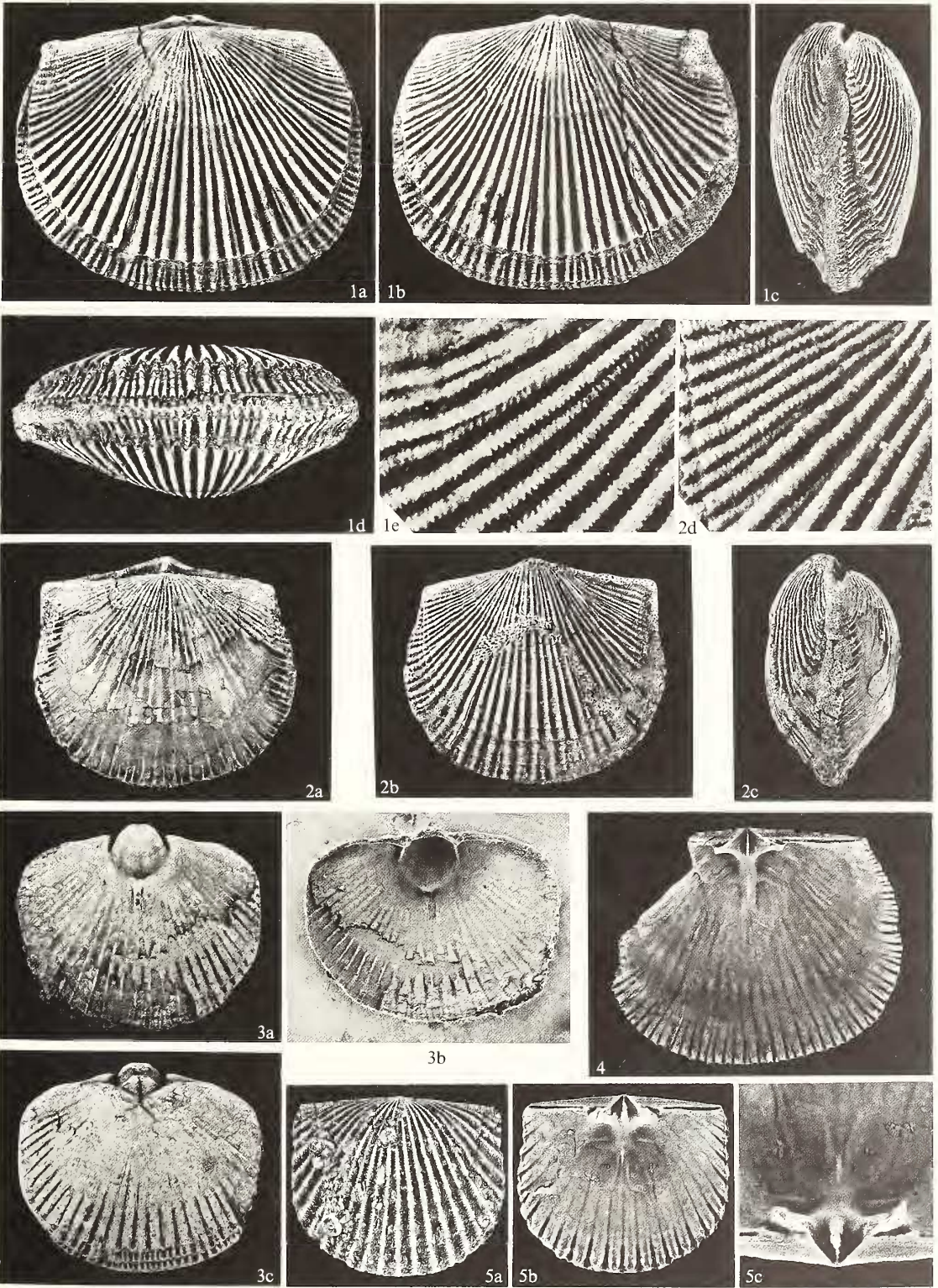
*Lectotype* (here selected). RM Br21959, Dalman Collection, dorsal valve, figured Pl. 8, fig. 1a–b; from Husbyfjöl, Östergötland, Sweden, zone of *Asaphus* (*Asaphus*) *expansus* ('Expansus Limestone'), high lower Ordovician (lower Kundan Stage, Hunderumian Substage – high *Didymograptus hirundo* to lowest *Didymograptus bifidus* Zone); the original specimen figured by Dalman (1828, pl. 2, fig. 2) and refigured by Hisinger (1837, pl. 20, fig. 9).

*Paralectotype.* RM Br21958, Dalman Collection, dorsal valve, figured Pl. 8, fig. 2; same locality and horizon as lectotype.

*Diagnosis.* Shell relatively large (maximum recorded length 30 mm). Costae low, rounded, widely spaced (OR 13–19). As the only confirmed species of the genus, other characteristic features of *O. callactis* apply equally to the generic diagnosis given above.

## EXPLANATION OF PLATE 9

- Figs 1–4. *Krattorthis verneuli* (Rubel, 1961). 1a–e, RM Br74764; Aserian Stage (C<sub>1</sub>a); Archangelskoje, Ingria, Russia; dorsal, ventral, lateral and anterior views of conjoined valves, with detail of lamellose micro-ornament on left lateral flank of dorsal valve, a–d × 2, e × 5. 2a–d, RM Br74424; probably Aserian Stage; Pulkova, Ingria, Russia; dorsal, ventral and lateral views of conjoined valves, with detail of lamellose micro-ornament on left lateral flank of ventral valve, a–c × 2, d × 5. 3a–c, RM Br74014; horizon and locality as Fig. 2; conjoined valves with shell heated and scraped away to reveal interiors, ventral valve with latex cast, dorsal valve, × 2. 4, RM Br74762; Aserian Stage (C<sub>1</sub>a); Duboviki, Ingria, Russia; interior of dorsal valve, × 2.
- Fig. 5. *Glossorthis tacens* Öpik, 1930. 5a–c, RM Br68424; Uhakuan Stage (C<sub>1</sub>cβ); Türpsalu, Estonia; exterior and interior of dorsal valve, with posterior view of cardinalia, distal portion of brachiophores not preserved, a–b × 2, c × 4.



JAANUSSON and BASSETT, *Krattorthis*, *Glossorthis*

*Distribution.* *O. callactis* is known with certainty only from the lower Kundan beds (zone of *A. expansus*) in Baltoscandia (Östergötland, Öland, and Siljan district in Sweden; lower Voka beds of north-western Estonia; and Ingria).

Genus KRATTORTHIS gen. nov.

*Type species.* *Glossorthis verneuili* Rubel, 1961; from the upper Kundan and Aserian Stage (Llanvirn) of northern Estonia and Ingria, Russia.

*Derivation of name.* Kratt, a kind of troll in Estonian folklore.

*Diagnosis.* Subequally biconvex to slightly ventribiconvex, multicostellate with densely spaced, distinct concentric to lamellose fila. Interareas very short, anterior commissure rectimarginate. Dental plates slender, ventral muscle field situated on an elevated platform with a rounded anterior margin which is produced only slightly anterior to the delthyrial cavity. Cardinalia relatively small and delicate; brachiophore process slender, somewhat flattened laterally and slightly curved posteroventrally, supported by plates which are undercut and converge dorsomedially onto a ridge; cardinal process high and slender. Shells relatively large.

*Remarks.* *Krattorthis verneuili* is a distinctive, relatively large (known maximum length 23 mm) and fairly common species that was first figured by Verneuil (*in* Murchison *et al.* 1845, pl. 13, figs 11a–c) but referred incorrectly by him to *Orthis extensa* Pander, 1830; the latter species was described originally as a *Productus* and belongs to *Panderina* (see Schuchert and Cooper 1932, p. 78, n. 38). Schuchert and Cooper (1932, p. 78) referred *O. extensa sensu* Verneuil *non* Pander to *Glossorthis*. However, the specimen figured by them (1932, pl. 4, figs 3, 6, 10) has a distinct dorsal sulcus and is stated to come from much older beds (B<sub>2</sub>; upper Arenig Volkhov Stage). We have not observed a comparable dorsal sulcus among the numerous examined specimens of *K. verneuili*. Rubel (1961, p. 184, pl. 18, figs 5–10) named the species figured by Verneuil *Glossorthis verneuili* nom. nov., but in reality he established a new species and the type designated by him is a holotype not a neotype.

It is possible that the specimen named and figured by Pander (1830, pl. 16A, fig. 4) as *Orthambonites*, but without a description, is a synonym of *K. verneuili*. This is suggested particularly by the very short interareas, not known in any other biconvex orthacean from Ingria. The size and relative convexities of the valves are also similar, although the multicostellate ornament of Pander's figure appears to be irregular and finer than that in *K. verneuili*. Although the name *O. dubia* is valid as an indication under Article 12(b)(7) of the ITZN Code (1985), we propose that it should be treated as a *nomen oblitum* in terms of previous editions of the code since its senior synonymy cannot be proved and the name *verneuili* has now become established in the literature based on a validly designated type specimen.

Externally *Krattorthis* differs from *Glossorthis* in its much finer multicostellate ornament and far more strongly convex dorsal valve. For a full description of the external characters of *K. verneuili* see Rubel (1961, p. 184, pl. 18, figs 5–10).

The interior of *K. verneuili* has not been described previously, but examination of a well-preserved dorsal interior collected by G. Holm (Pl. 9, fig. 4) confirms that it differs from *Glossorthis*, and this is supported further by preparations of ventral interiors (Pl. 9, figs 3a–b). The ventral muscle field forms an anteriorly-elevated platform but it lacks a tongue-like anterior projection (Pl. 9, fig. 3b). A characteristic feature for *Glossorthis* is the position of the maximum length of the hinge-teeth far lateral of the delthyrial margins, associated with a distinct growth line which defines a triangular area on the interarea (Schuchert and Cooper 1932, p. 79). No free ventral valves of *K. verneuili* have been available and it is not known whether the hinge-teeth in *Krattorthis* have a similar position relative to the delthyrial margins. However, no comparable growth line on the interarea has been observed. The cardinalia of *K. verneuili* are remarkably small relative to the size of the valve (Pl. 9, fig. 4), much smaller than in *Glossorthis* (Pl. 8, fig. 11; Pl. 9, fig. 5b–c).

In all figured dorsal interiors of *Glossorthis* (Öpik 1930, pl. 3, figs 28–32, pl. 4, figs 34, 36, 39;

Schuchert and Cooper 1931, pl. 4, fig. 8; Alikhova *in* Sarycheva 1960, pl. 12, fig. 8; Williams *et al.* 1965, fig. 194:8*b*) the brachiophore processes appear to be partly or completely broken off, as they are in the majority of specimens examined by us (see also Pl. 8, fig. 11). In addition, the broken ends of the processes in most specimens have been worn by depositional processes or, when exposed, to recent subaerial weathering. This gave an impression in the past that in *Glossorthis* the brachiophores are 'blunt, rather short' (Schuchert and Cooper 1932, p. 78). Preparation of a juvenile dorsal valve of *Glossorthis tacens* revealed a virtually complete brachiophore process (Pl. 9, figs 5*b–c*). It is fairly long, laterally flattened and with a distinct posteroventral curvature. In *Krattorthis verneuili* (Pl. 9, fig. 4) the process is subtriangular in cross section with a medially flattened surface; it is narrower than in *Glossorthis tacens* and only slightly curved posteroventrally. The brachiophores are supported by plates that converge onto a median ridge; they are undercut and resemble the plectorthid type. In *Glossorthis* the brachiophores are supported by adventitious shell substance which forms a prominent notothyrial platform (Pl. 8, fig. 11).

*Occurrence.* As currently known the genus is monotypic. Rubel (1961, p. 185) gave data on the distribution of *K. verneuili* in middle Llanvirn equivalent strata of northern Estonia and Ingria (Aluojan Substage of the Kundan Stage, and the Aserian Stage).

#### APPENDIX: OTHER SPECIES ASSIGNED PREVIOUSLY TO *ORTHAMBONITES*

##### 1. *Pander's (1830) species*

Of the 18 species originally named by Pander as *Orthambonites*, it is likely that no more than five belong in the genus as now restricted in this paper. Even within these we emphasize that their identification remains only tentative, based on a typological assessment of Pander's illustrations and brief descriptions, but supported by a comparison with the collections from Ingria available to us. Of the five, we have commented earlier (pp. 23–26, 33) on relationships and the possible synonymy groupings of *O. rotunda*, *O. lata*, *O. aequalis*, and *O. semicircularis*. Pander considered that *O. plana* (1830, p. 82, pl. 22, fig. 8*a–d*) is very similar to *O. semicircularis*, but *plana* has fewer primary ribs (21) and is less convex, so that we doubt the similarity and consider its generic relationships to remain uncertain. In addition, *O. ovata* Pander, 1830, p. 85, pl. 16*A*, fig. 9 has the convexity and general costate ribbing pattern (23 ribs) of *Orthambonites*, and its suboval outline may be an end-variant in the range of shape displayed by one of Pander's other taxa.

We have also commented on *O. transversa*, which is the previously designated type species of *Orthambonites*, but which we propose should be regarded as a *nomen dubium*, and on *O. tetragona* and *O. rotundata* which are probably synonyms and represent a *Glossorthis*-like form. *Orthambonites dubia*, figured but not described by Pander, resembles *Krattorthis verneuili*, and we propose here (p. 56) to regard it as a *nomen oblitum*.

Alikhova (1953, p. 28) suggested that *O. crassicosta* Pander, 1830, p. 82, pl. 21, fig. 1 and *O. eminens* Pander, 1830, p. 82, pl. 21, fig. 2 are junior synonyms of *Orthis callactis* Dalman, 1828, and this appears to be probable (see synonymy, p. 54). Pander's figures of *Orthambonites convexa* (1830, p. 82, pl. 25, fig. 8) and *O. alta* (1830, p. 82, pl. 25, fig. 17) show a *Nicolella*-like exterior and should be considered when Ingrian species of early *Nicolella* are revised. Pander himself pointed out that *Orthambonites flexuosa* (1830, p. 83, pl. 16*B*, fig. 8) differs in several characters from other species of *Orthambonites*; it is clearly a clitambonitacean.

Three further species included by Pander (1830, p. 83) in *Orthambonites* were assigned only with some hesitation. Of these, *O. parva* Pander, p. 83, pl. 26, fig. 10 was subsequently made the type species of the enteletacean genus *Paurorthis* Schuchert and Cooper, 1931, p. 231 (see also Schuchert and Cooper 1932, p. 79, pl. 3, figs 5–8, 10; Öpik 1933, p. 12, pls 3–4; pl. 5, fig. 4; neotype designated by Rubel 1961, p. 196). Schuchert and Cooper (1932, p. 79) also assigned *Orthambonites trigona* Pander, p. 83, pl. 26, fig. 11 to *Paurorthis*. The relationships of the third species, *O. sphaerica* Pander, 1830, p. 84, pl. 16*B*, fig. 11, remain unclear.

It is beyond the scope of this paper to discuss these relationships further; in each case, the identity and use of Pander's species names should await a full taxonomic study of the relevant groups based on collections from Pander's type area in Ingria, and involving the designation of neotypes as appropriate in order to stabilize the concept of the various taxa.

##### 2. *Species excluded from Orthambonites*

Several species assigned originally to *Orthambonites* have either been transferred subsequently by other authors to other genera, or do not appear to us to belong to the genus or to any of the related genera described in this paper.

*Orthambonites bifurcatus* Cooper, 1956, p. 297, pl. 34, figs 1–6, from the upper Pogonip Group (Whiterock), Nevada, USA (see also Ross 1970, p. 54, pl. 3, fig. 20) was assigned by Neuman (*in* Neuman and Bruton 1974, p. 78, fig. 7A–K) to *Trondorthis*.

*Orthambonites brachiophorus* Cooper, 1956, p. 298, pl. 36, figs 32–39; from the Effna and Rich Valley Formations, Virginia, USA was assigned by Jaanusson and Bergström (1980, p. 98) to *Dolerorthis*. In this species the relative length of the ventral interarea, the general type of ribbing, the conspicuous concentric fila, and particularly the structure of the brachiophores and the thin cardinal process so closely resemble those of some north-west European middle Ordovician species currently referred to *Dolerorthis*, that we have little doubt that they are congeneric.

*Orthambonites neumani* Cooper, 1956, pl. 37, figs 19–28, is from the Tellico Formation, Tennessee, USA. This species (maximum known length 19 mm) closely resembles *Dinorthis* in its internal characters but differs externally in having a strongly convex ventral valve (Cooper 1956, p. 308); its affinities may be with the Plaesiomyidae. The long, lobate ventral muscle field, the presence of conspicuous concentric fila, and the relatively long ventral interarea distinguish it from *Orthambonites*. Williams (1962, p. 100) pointed out similarities between *O. neumani* and *Orthis* (*Plectorthis*) *subplicatella* Reed, 1917 (Williams 1962, pl. 8, figs 12–14) from the Balclatchie Mudstones of the Girvan district, but the characters of the latter species remain too poorly known to allow a firm generic reference to be made.

*Orthambonites tuloicens* Andreeva, 1982, p. 54, pl. 3, fig. 6-3, from the Stretinskaya(?) Formation (middle Ordovician?), Altai region, USSR, is certainly not *Orthambonites*. Its affinities appear to be with *Hesperorthis* as witnessed particularly by the long ventral interarea, the narrow delthyrium, and the position of the hinge teeth set somewhat lateral to the delthyrial margin (Andreeva 1982, pl. 3, fig. 7).

*Orthambonites? inaequalis* Rubel, 1961, p. 179, pl. 12, figs 8–10, is from the Kundan Stage, northern Estonia. The flat, faintly sulcate dorsal valve, comparatively short cardinalia, and the micro-ornament consisting solely of distinct concentric fila, exclude this species from *Orthambonites*. Further knowledge of internal morphology is required before its generic assignment can be determined.

*Orthambonites rognebrunensis* Melou, 1982, p. 27, pl. 4, figs 1–5 from the lower Schistes de Landeyran (Arenig), Montagne Noire, France, may be related to *Paralenorthis*, but differs in having pronouncedly costellate ribbing, a longer, anteriorly bilobate ventral muscle field, and a poorly-defined cardinal process. It cannot be assigned confidently to any known genus.

### 3. Species requiring further investigation

There is, finally, a small group of species that we have encountered in the literature that were either identified originally by their authors as *Orthambonites* or were transferred subsequently to the genus, but which we believe to be too poorly known to allow any meaningful comments to be made as to their relationships. For the most part these species are based on poorly preserved material or are described and illustrated inadequately; additional taxonomic investigation of either the original material or of new collections would be necessary to comment further on these forms, which are recorded here to complete the coverage of literature dealing with previous interpretations of *Orthambonites*. On balance, the limited information available suggests to us that it is unlikely that any of these species belongs within the genus.

*Orthis decipiens* Phleger, 1933, p. 17, pl. 1, fig. 2; Barrel Spring Formation (Whiterock), California, USA. Assigned by Ross (1967, p. D2, pl. 1, figs 31–36) to *Orthambonites*, although Cooper (1956, p. 351) questionably assigned it to *Hesperorthis*.

*Orthambonites divaricatus* Cooper, 1956, p. 302, pl. 33, figs 1–3; Effna and Rich Valley Formations, Virginia, USA.

*Hebertella exfoliata* Raymond, 1905, p. 370; Day Point Formation, New York State, USA. Assigned tentatively to *Orthambonites* by Cooper (1956, p. 303), although he suggested that the external morphology resembles that of *Desmorthis*.

*Orthambonites fraternus* Havlíček, 1971, p. 31, pl. 3, figs 7–10, pl. 23, fig. 3; Llandeilo beds, Morocco.

*Orthambonites jaboganicum* Severgina, *in* Petrunina and Severgina 1962, p. 88, pl. 3, figs 1–4; Khankharinsky Group (Caradoc), Altai Mountains, USSR (see also Kulkov and Severgina 1989, p. 65, pl. 8, figs 15–18).

- Orthambonites tuvensis* Andreeva, 1982, p. 53, pl. 3, figs 1–5; Tarlyk Formation (?Whiterock), Tuva, Russia.  
*Orthambonites planus* Bondarev, 1968, p. 65, pl. 1, figs 1–4; Yngor beds (middle Ordovician), Vaigach and Pai-Khoy, Russia.  
*Orthambonites pseudomonetus* Bednarczyk, 1964, p. 63, pl. 12, figs 1–4, 7, 8, 13; Bukówka and Dyminy beds (lower Ordovician), Kielce region, Holy Cross Mountains, Poland.

*Acknowledgements.* For providing information and for allowing us to study collections in their care we thank Dr G. A. Cooper and Mr F. J. Collier (United States National Museum, Washington), Dr L. E. Popov (VSEGEI, St Petersburg), Dr L. Hintz and Dr M. Rubel (Institute of Geology, Estonian Academy of Sciences, Tallinn), and Professor G. Henningsmoen and Dr D. L. Bruton (Paleontologisk Museum, Oslo). Dr R. B. Neuman (Washington) and Dr R. J. Ross Jr. (Denver) kindly discussed with M. G. B. some taxa with which they were particularly familiar, Dr Rong Jia-Yu similarly gave helpful advice and allowed examination of collections in the Institute of Geology and Palaeontology, Nanjing, and Dr D. A. T. Harper (Galway) gave practical help in the computation of statistics. The Soviet Academy of Sciences and Estonian Academy of Sciences generously funded studies in the Soviet Union by M. G. B., whose participation in the work for this paper was also supported by the National Museum of Wales, the Swedish Museum of Natural History (Erik Stensiö Palaeozoology Fund), and the Swedish Natural Science Research Council (NFR Grant G-GF2247-101). Figured specimens are housed in the Department of Palaeozoology at the Swedish Museum of Natural History (RM), the Paleontologisk Museum, Oslo (PMO), the Institute of Geology of the Estonian Academy of Sciences, Tallinn (TAGI), the F. Chernychev Central Geological Research Museum, Leningrad (CNIGR), the Department of Paleobiology at the United States National Museum of Natural History, Washington (USNM), and the Department of Geology at the National Museum of Wales, Cardiff (NMW).

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V. JAANUSSON

Sektionen for Paleozoologi  
Naturhistoriska Riksmuseet  
S-104 05 Stockholm 50, Sweden

M. G. BASSETT

Department of Geology  
National Museum of Wales  
Cathays Park  
Cardiff CF1 3NP, UK

Typescript received 16 June 1991

Revised typescript received 20 February 1992

#### Note Added in Proof

Subsequent to the submission of the manuscript, we have noted two further species assigned to *Paralenorthis*, both described by Herrera and Benedetto (1989) from the lower Ordovician of the Argentinian Precordillera. *P. vulgaris* Herrera and Benedetto (1989, pl. 4, figs 8, 14–15, 20) shows distinctly the proximally separated and divergent vascula media typical of the genus (p. 34 herein); it is from late Arenig beds of the Huaco Anticline and upper levels of the San Juan Formation (early Llanvirn) in the Cerro Viejo Range. Their second species, recorded under open nomenclature, is also from the upper San Juan Formation, apparently occurring at a single locality in association with *P. vulgaris*; the authors comment that the material is too poorly preserved to make a specific determination, but suggest that the disposition of the vascula media support an assignment to *Paralenorthis*.

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